

THE VASCULAR FLORA OF LA SELVA BIOLOGICAL STATION,  
COSTA RICA\*  
POLYPODIOPHYTA

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GRAYUM, M. H. AND H. W. CHURCHILL. 1989. The vascular flora of La Selva Biological Station, Costa Rica. Lycopodiophyta. Selbyana 11: 61-65. (See references listed there.)

STOLZE, R. G. 1976. Ferns and fern allies of Guatemala. Part I. Ophioglossaceae through Cyatheaceae. Fieldiana, Bot. 39: 1-130.

Homosporous (ours), seedless vascular plants, all with *megaphylls* (mostly large leaves with several to many veins and the leaf trace associated

with a leaf gap). The *sporangia* are generally borne abaxially or marginally on ordinary or reduced foliage leaves. *Gametophytes* typically free-living and photosynthetic. These are the true ferns, a diverse and successful group with about 12,000 modern species (about two-thirds of which are tropical). The group comprises innumerable growth forms, ranging from minute, thallose epiphytes or floating aquatics to giant tree-ferns; both extremes occur at La Selva.

KEY TO THE FAMILIES

1. Sterile leaf one per shoot, simple, entire, erect or folded in veneration (not circinate); sporangia large, thick-walled, borne in two rows on a long-stalked spike subtended by the sterile leaf; small, terrestrial plants, very rare at La Selva. . . . . 1. OPHIOGLOSSACEAE.
1. Sterile leaves usually more than one, simple to compound, circinate in bud; sporangia borne on margin or abaxial surface of typical or modified foliage leaves; plants terrestrial, epilithic or epiphytic.
  2. Sori in marginal, cuplike or tubular involucre; plants usually tiny to small, delicate epiphytes with the laminae thalloid to finely dissected and more or less translucent, one to few cell layers thick (if relatively coarse and/or terrestrial, then each involucre with a hairlike, exserted receptacle). . . . . 4. HYMENOPHYLLACEAE.
  2. Sori not in marginal, cuplike involucre or, if so, the plants coarse and terrestrial; sori never with hairlike, exserted receptacles.
    3. Frond axes dichotomously branched, pinnately narrow-lobed; plants terrestrial, the rhizome long-creeping. . . . . 3. GLEICHENIACEAE.
    3. Frond axes not dichotomously branched or, if so, the plants epiphytic.
      4. Stipules present at base of petioles; fronds dimorphic, pinnate, the rachis nodose; pinnae opposite; sporangia fused laterally into synangia, lacking an annulus. . . . . 2. MARATTIACEAE.
      4. Stipules lacking; fronds di- or monomorphic, simple to compound, the rachis not nodose; pinnae on compound leaves alternate or, rarely, opposite; sporangia distinct, annulate.
        5. Annulus oblique, fully encircling the sporangium; plants usually arborescent, with distinct trunks more than 0.5 m tall in fertile individuals; fronds rarely pinnate or pinnate-pinnatifid, more frequently bipinnate-pinnatifid to 4-pinnate; petiole bases, trunks, etc., rarely unarmed, more typically spinose; sori (in ours) round, abaxial.
          6. Fronds simply pinnate, the pinna margins entire or apically serrulate; rhizome stout, creeping, densely covered with orangish trichomes, the plants completely scaleless and unarmed. . . . . 5. METAXYACEAE.
          6. Fronds pinnate-pinnatifid to 4-pinnate; rhizome generally arborescent (rarely obsolete); plants (especially the petiole bases) always scaly, typically armed with spines (rarely unarmed). . . . . 6. CYATHEACEAE.

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5. Annulus vertical, interrupted by the stalk of the sporangium; rhizome creeping to erect, occasionally subarborescent but only exceptionally (*Diplazium striatastrum*) more than 0.5 m tall; fronds simple to decomposed; petioles, etc., spinose only in *Hypolepis* (with creeping rhizome); sori highly variable in shape, abaxial to marginal. . . . . 7. POLYPODIACEAE.\*

\* N.B.: If the orientation of the annulus cannot be determined, two aberrant species of "tree-ferns," *Metaxya rostrata* (Metaxyaceae) and *Cyathea ursina* (Cyatheaceae), will key out here. Since these are not separable from Polypodiaceae by means of ordinary field characters, they are included in the generic key for that family as well.

### 1. OPHIOGLOSSACEAE

Small, terrestrial (at La Selva) herbs with short, subterranean rhizome. *Sterile leaf* solitary on the shoot, not circinate in vernation, sessile to short-stalked, simple to compound. *Fertile segments* one to several, non-foliaceous, spicate or paniculate, arising from the apex of a common stalk shared with the sterile lamina. *Sporangia* lacking an annulus, thick-walled, two-valved at maturity.

Three genera and about 50 species. *Botrychium* Sw. occurs mostly in Arctic and temperate regions and (as in Costa Rica) tropical mountains; it differs from *Ophioglossum* in its decomposed sterile and fertile laminae, and open venation.

#### 1. OPHIOGLOSSUM L.

GOMEZ P., L. D. 1976. Contribuciones a la pteridología costarricense. IX. El género *Ophioglossum* en Costa Rica. Brenesia 8: 85-95.

*Sterile lamina* simple and entire (in ours) or coarsely palmately lobed, with reticulate venation. *Fertile segments* consisting of one (in ours) to several stalked "spikes," bearing two rows of coalescent sporangia.

A pantropical and temperate genus of about 25 species, five of which occur in Costa Rica.

#### 1. *Ophioglossum reticulatum* L.

Terrestrial plants forming small to large colonies. *Rhizome* 0.4-1.9 cm long, horizontal to erect, with one or occasionally two shoots. *Common stalk* of sterile laminae and fertile segment 3-12 cm long. *Sterile lamina* reniform to cordate, ovate or elliptic, 2-6.3 cm long and 0.8-4.3 cm broad, rounded to apiculate or subacute apically, cuneate to truncate or cordate at base. *Fertile segment* 1.8-5.7 cm long and 2-3.5 mm wide, on a stalk 7-20.5 cm long. Southern Mexico to Bolivia and the West Indies, Old World tropics; widespread in Costa Rica from 0 to 2,000 m.

Very rare at La Selva, known from a few small populations in the grassy pejibaye clearing.

### 2. MARATTIACEAE

Terrestrial plants, generally with stout, erect rhizomes and compound leaves. *Leaves* circinate in vernation, stipulate, the laminar axes and (usually) the *petiole* with swollen nodes. *Sporangia* abaxial, thick-walled, lacking annuli, coalescent into elongate (in ours) synangia.

A well circumscribed and distinctive family, easily recognized by the fleshy stipules at the base of the petiole, swollen laminar nodes and synangia. About seven genera, two indigenous in the New World. Both of these, *Marattia* Sw. and *Danaea*, occur in Costa Rica, though only the latter is found at La Selva. *Marattia*, which differs from *Danaea* in its bi- to quadripinnate, usually solitary leaves, occurs at higher elevations.

#### 1. DANAEA J. E. Smith

UNDERWOOD, L. M. 1909. *Danaea*. North Amer. Flora 16: 17-21.

*Leaves* dimorphic, simple to (in ours) once-pinnate. *Veins* free and closely parallel. *Synangia* mostly covering the abaxial surface of the fertile pinnae.

A strictly neotropical genus of 20-30 species, ranging from Mexico to Bolivia and throughout the West Indies. About 9 species are known from Costa Rica.

Research at La Selva by J. Sharpe (pers. comm.) has shown the maturation of mature fronds in all our species of *Danaea* to be markedly seasonal.

#### KEY TO THE SPECIES

1. Fronds (lamina plus petiole) less than 40 cm long, often even-pinnate; very common. . . . . 5. *D. wendlandii*.
1. Fronds more than 40 cm long, always odd-pinnate; occasional to rare.
  2. Petiole lacking leafless nodes; rhizome and base of petiole magenta in cross-section.
    3. Petiole of sterile fronds more than 73 cm long; largest sterile pinnae more than 5 cm wide; pinnae of mature fronds 14 pairs or more; fertile fronds maturing in dry season (January-May); very rare. . . . . 3. *D. grandifolia*.
    3. Petiole of sterile fronds less than 73 cm long;

sterile pinnae less than 5 cm wide; pinnae fewer than 14 pairs; fertile fronds maturing in the wet season (July–September); occasional. . . . . 4. *D. nodosa*.

2. Petiole with 1–5 leafless nodes; rhizome and base of petiole white in cross-section.
  4. Sterile pinnae fewer than 7 pairs, broadly elliptic, more than 2.5 cm wide, green below, entire throughout; rhizome often briefly caulescent; occasional. . . . . 2. *D. elliptica*.
  4. Sterile pinnae more than 7 pairs, linear-oblong, less than 2.5 cm wide, silvery-white below, serrulate toward apex; rhizome obsolete; very rare. . . . . 1. *D. cuspidata*.

1. ***Danaea cuspidata* Liebman.**  
(=*D. munchii* Christ)

*Petiole* 17–44 cm long. *Sterile lamina* 30–60 cm long, with 8–18 pairs of pinnae. *Sterile pinnae* linear to narrowly oblong, silvery below, strongly serrulate and acuminate apically, 9–16 cm long, 1.5–2.5 cm wide. *Fertile pinnae* linear, 4–8 cm long, 4–8 mm wide. The fertile fronds mature from January to March. Oaxaca to Panama; the most widespread *Danaea* in Costa Rica, ranging from 0 to 2,300 m.

*Danaea cuspidata* is known at La Selva from just a few plants along the Q. El Salto near Line 3200. It is also common on steep slopes along the R. Peje.

2. ***Danaea elliptica* J. E. Smith**

*Rhizome* obsolete to subarborescent (to about 30 cm tall). *Petiole* 16–35 cm long (or longer on fertile fronds). *Sterile lamina* 20–35 cm long, with 3–7 pairs of pinnae. *Sterile pinnae* elliptic, 8–26 cm long, 2.5–6 cm broad. *Fertile pinnae* 5.5–12.5 cm long, 1.5–3 cm wide. The fertile fronds mature from July to November. Southern Mexico to Bolivia, West Indies; from 50 to 800 m on the wetter parts of the Caribbean slope in Costa Rica.

Occasional at La Selva on ridges and hilltops in primary forest.

3. ***Danaea grandifolia* L. Underw.**

*Petiole* about 80–110 cm long; sterile lamina about 80–95 cm long, with 14–17 pairs of pinnae. *Sterile pinnae* 25–45 cm long, 5.5–8.2 cm broad, the lowermost stalked to 1.5 cm. *Fertile pinnae* to ca. 25 cm long, 2.5–3.5 cm broad, short-stalked. The fertile fronds mature from January to May. Costa Rica to Colombia (Chocó); La Selva and Finca El Bejuco, near Chilamate, are the only known Costa Rican stations for this fern.

At La Selva, *Danaea grandifolia* is known from

just two populations: a large one along the Q. Pantano at about Line 2100, and a much smaller one in the vicinity of CES 450.

This rare fern is similar in most respects to *Danaea nodosa*, with which it has sometimes been lumped, but considerably larger; in life it appears as distinctive as do most species of *Danaea*.

4. ***Danaea nodosa* (L.) J. E. Smith**

*Petiole* 29–61 cm long. *Sterile lamina* about 40–70 cm long, generally with 6–13 pairs of pinnae. *Sterile pinnae* narrowly elliptic or oblong, 18–26(–35) cm long, 2.5–3.5 cm wide, entire or bluntly serrulate and acuminate apically. *Fertile pinnae* about as long, but narrower. The fertile fronds mature from July to September. Southern Mexico to Brazil, West Indies; from 0 to 1,100 m in Costa Rica, on both slopes.

Occasional at La Selva, usually in low, damp areas in primary forest.

5. ***Danaea wendlandii* Reichb. f.**

*Rhizome* short-creeping to suberect. *Petioles* 2.5–10 cm long (–18 cm on fertile fronds), with 0–1 leafless nodes. *Sterile lamina* 9–18 cm long, odd- or even-pinnate with 10–13 pairs of pinnae, often viviparous at the terminal node. *Rachis* narrowly winged. *Sterile pinnae* narrowly oblong, 2–5 cm long and 6–12 mm broad, finely serrate apically. *Fertile pinnae* 1.1–1.8(–2.4) cm long, 2–6 mm wide. Fertile fronds mature from March to September. Costa Rica to Colombia (Chocó); from 0 to 700 m on the Caribbean coast of Costa Rica.

Our smallest and most common *Danaea*, widespread in the understory of primary forest.

### 3. GLEICHENIACEAE

MAXON, W. R. 1909. Gleicheniaceae. North Amer. Flora 16(1): 53–63.

Usually somewhat weedy terrestrial ferns with slender, long-creeping *rhizomes* and dichotomously branching fronds with dormant axillary buds. *Fronds* circinate in veneration, of indeterminate growth, often very long and subscentent. *Penultimate segments* in our species deeply pinnatifid, with the lobes entire. *Venation* free. *Sporangia* round, exindusiate. *Annulus* oblique, transverse or apical, not interrupted by the stalk of the sporangium.

A pantropical family of two genera, both of which are represented in the greater La Selva area.

KEY TO THE GENERA

- 1. Rhizomes and laminar buds with trichomes, not scaly; veins of the ultimate segments 2- to 4-forked; lamina (in ours) glaucous below; very rare. . . . . 1. *DICRANOPTERIS*.
- 1. Rhizomes and laminar buds with scales; veins of the ultimate segments simple or 1-forked; lamina (in ours) green below; occasional. . . . . 2. *GLEICHENIA*.

1. *DICRANOPTERIS* Bernh.

Characters of the family (separated from *Gleichenia* by the characters in the key). A pantropical genus of about 10 species, only two of which occur in Costa Rica. The other Costa Rican species, *D. flexuosa* (Schrader) L. Underw., has been collected near Chilamate.

1. *Dicranopteris pectinata* (Willd.) L. Underw.

*Petiole terete*, straw-colored to light brown, mostly glabrous. *Lamina* branching in a pseudodichotomous fashion, the branches flexuous. *Penultimate segments* lanceolate, 8–25 cm long, 1.5–6.5 cm broad, pectinate, glaucous below. Guatemala to Bolivia and the West Indies; widespread in Costa Rica from 0 to 1,800 m.

Clambering and often forming thickets on slopes in well-lit places. *Dicranopteris pectinata* is not known from La Selva proper, but has been collected along the R. Peje just off the property.

2. *GLEICHENIA* J. E. Smith

Characters of the family; separated from *Dicranopteris* by its scaly rhizomes and laminar buds, and simple or once-forked veins. As conservatively treated, a pantropical genus of 110–130 species. Some workers would split off *Diplopterygium* (Diels) Nakai and *Sticherus* C. Presl, the latter of which would include virtually all of the New World species, and all 14–16 Costa Rican species with the exception of *G. bancroftii* (Hook.) L. Underw.

1. *Gleichenia bifida* (Willd.) Sprengel  
(=*Sticherus bifidus* (Willd.) Ching)

*Petiole* stout, erect, glabrous, terete, yellowish to greenish-brown. *Lamina* pseudodichotomously branched. Tertiary axes and *penultimate segments* pectinate, the latter 15–60 cm long, 2–7 cm wide, densely and evenly tomentose below with orangish, stellate trichomes. *Costa* below with conspicuous, spreading orange scales. Mexico to Bolivia, West Indies; widespread in Costa Rica from 0 to 2,200 m.

Occasional at La Selva in disturbed sites along river banks, and in light gaps in primary forest.

4. HYMENOPHYLLACEAE

MORTON, C. V. 1968. The genera, subgenera, and sections of the Hymenophyllaceae. *Contr. U.S. Natl. Herb.* 38: 153–214.

Extremely variable in habit; terrestrial to epiphytic, with the *rhizome* erect to long-creeping. Plants generally small to minute, with thin, filmy and often translucent laminae, occasionally coarser with thicker, opaque laminae. *Leaves* circinate in veneration, lacking stipules, the *venation* usually free. *Sori* marginal, borne in cup-like or tubular indusia. *Annulus* oblique (not interrupted by the stalk of the sporangium).

A fundamentally pantropical family, with a few extensions into temperate regions. The Hymenophyllaceae are generally treated as comprising two large genera, each with several subgenera. Some prefer to divide the assemblage more finely, however, and as many as 42 genera have been distinguished.

KEY TO THE GENERA

- 1. Receptacle filiform or thicker, not exerted from the indusium; indusium bivalvate, lacking a basal tubular portion. . . . . 1. *HYMENOPHYLLUM*.
- 1. Receptacle filiform, becoming obviously exerted from the indusium; indusium tubular in at least the basal half, usually apically bilabiate. . . . . 2. *TRICHOMANES*.

1. *HYMENOPHYLLUM* J. E. Smith

MORTON, C. V. 1947. The American species of *Hymenophyllum* section *Sphaerocionium*. *Contr. U.S. Natl. Herb.* 29: 139–201.

Plants (at La Selva) always epiphytic, the *rhizome* long-creeping. *Fronde* monomorphic, pinnately divided to decompose. *Venation* always free. *Indusium* bivalvate, the receptacle rarely exerted.

Species of *Hymenophyllum* are rather uniform in appearance compared with those of *Trichomanes*, and are consequently more difficult taxonomically.

A pantropical genus of about 300 species (as here treated), ranging in the New World from southeastern Alaska to Tierra del Fuego, and throughout the West Indies. About 30–32 species are known from Costa Rica, mostly from above 1,000 m.

KEY TO THE SPECIES

- 1. Fertile frond (including the stipe) less than 1.5 cm long; rare canopy epiphyte. . . . . 1. *H. brevifrons*.

1. Fertile fronds more than 1.5 cm long.
2. Lamina with bifid or stellate, frequently dark-colored trichomes, at least marginally, in the sinuses, or along the rachis.
3. Petiole alate to the base; trichomes abundant along veins, mostly 2-several times branched. . . . . 2. *H. hirsutum*.
3. Petiole alate only in the apical portion; trichomes lacking or sparse along veins, mostly simple and 1-forked. . . . . 3. *H. maxonii*.
2. Lamina completely glabrous, or with a few minute, simple hairs. . . . . 4. *H. polyanthos*.

### 1. *Hymenophyllum brevifrons* Kunze

Mat-forming branch epiphytes, the *rhizome* thin and delicate. *Petiole* glabrous, delicate, ca. 1–8 mm long. *Lamina* generally 0.5–1 cm long and 0.4–1 cm wide, reniform or ovate to obovate in outline, often truncate basally, pinnately or flabellately lobed, the lobes ascending. *Sori* 1–3 per frond. Guatemala and Belize to the Guianas and West Indies; ranging in Costa Rica from 0 to 1,300 m or higher on the Caribbean slope.

This is our smallest *Hymenophyllum*, and one of our smallest ferns. *H. brevifrons* has been collected only once at La Selva, as a canopy epiphyte in the platform *Lecythis* tree along the Camino Experimental Sur. It is no doubt more widespread in such situations.

### 2. *Hymenophyllum hirsutum* (L.) Sw.

*Petiole* 0.8–3 cm long, conspicuously alate usually to the base, pilose with mostly stellate hairs. *Lamina* narrowly ovate to oblong-lanceolate, 3–10 cm long and ca. 2–4 cm broad, pinnately divided; bifid *trichomes* scattered along the rachis, main veins, laminar margins and margins of the indusial valves. Southern Mexico to Bolivia and the West Indies; from 0 to 1,500 m in Costa Rica, on both coasts.

At La Selva *Hymenophyllum hirsutum* is apparently rather rare; it is known by just a few collections, from logs and low trunks in primary forest. Perhaps it is more common in the high canopy.

### 3. *Hymenophyllum maxonii* Christ ex C. Morton

*Petioles* filiform, 5–20 mm long, sparsely hairy, alate only in the apical ¼ to ½. *Lamina* ovate to narrowly lanceolate, 2–10 cm long, 1.5–4 cm broad, pinnately divided; simple to bifid *trichomes* scattered along laminar margin and margins of indusial valves. Southern Mexico and Guatemala; not heretofore reported from Costa Rica.

Common epiphyte in primary forest, frequently in the understory. This and *H. polyanthos* are our most common species of *Hymenophyllum*; they frequently grow together and may be mixed in collections, sometimes along with similar species of *Trichomanes* such as *T. krausii* and *T. diaphanum*.

In its apically forked rather than basally forked or stellate trichomes, our material is a better match for *Hymenophyllum maxonii* than it is for *H. microcarpum* Desv. (a closely related species that is widespread in Costa Rica). The former name is employed here with considerable trepidation, however, since *H. maxonii* has previously been reported only from mid-elevations in northern Mesoamerica.

### 4. *Hymenophyllum polyanthos* (Sw.) Sw.

*Petiole* 0.8–5 cm long, glabrous to sparsely pubescent, usually marginate or alate to near the base (the wings may be deciduous). *Lamina* ovate or deltate, 3–12 cm long, 2–6 cm broad, pinnately decomposed, generally glabrous throughout. Southern Mexico to Bolivia, West Indies; Africa and East Asia. It is widespread, from 0 to 2,900 m, in Costa Rica.

Common epiphyte on branches in primary forest, frequently seen in the understory. Some La Selva collections (e.g., Hammel 11118) approach the doubtfully distinct *Hymenophyllum myriocarpum* Hook. in their elongate leaf shape.

## 2. TRICHOMANES L.

WESSELS BOER, J. G. 1962. The New World species of *Trichomanes* sect. *Didymoglossum* and *Microgonium*. Acta Bot. Neerl. 11: 277–330.

Epiphytic or (less commonly) terrestrial plants, the *rhizome* long-creeping to erect. *Fronde* ranging from minute, simple and thalloid to moderately large and pinnatifid to decomposed, monomorphic or (less frequently) dimorphic. *Venation* free, or occasionally reticulate. *Indusium* tubular at least basally, the threadlike receptacle usually conspicuously exerted.

A pantropical genus of about 300 species, with some extensions into temperate regions. About 111 species range, in the New World, from western Massachusetts to Chile, and throughout the West Indies. The Costa Rican species number about 36; at least three additional species occur in the Sarapiquí region, and are to be expected at La Selva.

The species of *Trichomanes* at La Selva range from minute, epiphytic, thalloid organisms scarcely recognizable as vascular plants (e.g., *T.*

*angustifrons*, *T. godmanii*) to fair-sized, terrestrial, typically fernlike plants (*T. elegans*). All are nonetheless easily distinguished from *Hymenophyllum* (and all other La Selva ferns) by the hairlike receptacle protruding from the indusium. Though obvious in the field, these receptacles are delicate and easily broken, and hence may be lacking on herbarium material.

## KEY TO THE SPECIES

1. Plants terrestrial; sterile lamina deeply pinnately lobed to tripinnate.
  2. Lamina tri- to quadripinnate, opaque; fronds monomorphic; occasional to rare.
    3. Rachis and upper part of petiole continuously winged; lips of involucre flaring; occasional. . . . . 9. *T. elegans*.
    3. Rachis and upper part of petiole terete, or the rachis discontinuously narrow-winged; lips of involucre erect; extremely rare. . . . . 15. *T. rigidum*.
  2. Sterile lamina deeply pinnatifid to pinnate, translucent; fronds mono- or dimorphic; very rare.
    4. Lamina fully pinnate, the fronds monomorphic; veins of pinnae open, connected by short cross-veins. . . . . 14. *T. pinnatum*.
    4. Lamina deeply pinnatifid, the fronds dimorphic.
      5. Rachis of fertile fronds broadly alate, the sori attached at the margin of the wing; veins anastomosing. . . . . 7. *T. diversifrons*.
      5. Rachis of fertile fronds naked or essentially so, the sori attached directly thereto; veins open. . . . . 13. *T. osmundoides*.
1. Plants epiphytic or epilithic; lamina simple and entire to tripinnate-pinnatifid.
  6. Laminae tightly ventrally appressed to bark of supporting tree trunk, deeply pinnately lobed; very rare.
    7. Larger pinnae 7–12 mm wide, crenate; lips of involucre erect. . . . . 16. *T. tuerckheimii*.
    7. Larger pinnae 4–6 mm wide, serrate; lips of involucre flaring. . . . . 2. *T. ankersii*.
  6. Laminae widely divergent from supporting surface, entire to variously divided.
    8. Lamina pinnate to bipinnate-pinnatifid to the midrib (which may be alate) into linear or lanceolate segments.
      9. Rhizome erect to suberect, the fronds approximate; lamina once-pinnate, the pinnae subentire; petiole with spreading, slender, brownish, translucent trichomes; lamina pubescent with simple trichomes. . . . . 4. *T. crispum*.
      9. Rhizome long-creeping, the fronds distant; lamina pinnate-pinnatifid to bipinnate-pinnatifid, at least some pinnae deeply lobed; petiole glabrous or with stubby, dark, opaque hairs; lamina glabrous or with branched or stellate hairs.
        10. Frond (including stipe) more than 15 cm long; coarse plants, the stipe more than 1 mm thick at the base, the rhizome more than 1 mm thick. . . . . 3. *T. collariatum*.
        10. Frond less than 15 cm long; delicate plants, stipe (at base) and rhizome always less than 1 mm thick.
          11. Lamina with bifid or stellate, frequently dark-colored trichomes, at least marginally, in the sinuses or along the rachis; indusial valves dark-edged. . . . . 11. *T. krausii*.
          11. Lamina completely glabrous, or with a few minute, simple trichomes; indusial valves uniformly green. . . . . 6. *T. diaphanum*.
    8. Lamina entire to somewhat lobed, but never to the midrib.
      12. Lamina margin bearing paired, suborbicular marginal scales (these falling off on older fronds); fronds fairly large, at least some more than 3.5 cm long and/or more than 2.5 cm wide. . . . . 12. *T. membranaceum*.
      12. Lamina margins lacking paired, suborbicular scales; fronds rarely if ever more than 3.5 cm long or more than 2.5 cm wide.
        13. Margins of lamina with conspicuous forked or stellate trichomes; involucre lips with broad to thin dark border.
          14. Lamina linear to oblong, less than 5 mm wide; venation pinnate; involucre 1–3 per frond. . . . . 1. *T. angustifrons*.
          14. Lamina ovate to circular or obovate, more than 5 mm wide; venation flabellate; involucre frequently more than 3 per frond. . . . . 5. *T. curtii*.
  13. Margins of lamina glabrous, or with few simple hairs; involucre lips uniformly green.
    15. Lamina suborbicular, about as wide as long, entire to shallowly crenately lobed; venation reticulate, with obvious cross-veins; virtually restricted to trunks of the palm, *Welfia georgii*. . . . . 10. *T. godmanii*.
    15. Lamina obovate to oblanceolate, longer than wide, irregularly lobed, sometimes quite deeply; venation open, lacking cross-veins; not growing on *Welfia georgii*. . . . . 8. *T. ekmanii*.

1. *Trichomanes angustifrons* (Fée) W. Boer

Epiphyte, the *rhizome* delicate, creeping. *Petiole* obsolete to ca. 2 mm long. *Lamina* linear to oblong, 0.3–1.5 cm long, mostly 1–3 mm wide, usually entire or nearly so, thin and translucent, the margin with stellate hairs. *Sori* generally solitary, the indusial valves dark-edged. Costa Rica to Paraguay, West Indies; ranging from 0 to 400 m in Caribbean and southwestern Costa Rica.

This and *Hecistopteris pumila* are our smallest ferns. *Trichomanes angustifrons* is an understory trunk epiphyte, scattered in primary forest on both alluvial and upland sites.

2. *Trichomanes ankersii* C. Parker ex Hook. & Grev.

Epiphyte, the *rhizome* long-creeping. *Petiole* obsolete to about 3 mm long. *Lamina* ovate-lanceolate in outline, 4–14 cm long, 2.5–8 cm broad, pinnately divided to near the rachis. *Pinnae* narrowly lanceolate, the longest 1.5–5 cm long and 4–6 mm wide, spreading horizontally, the margins subpectinately toothed. *Sori* conspicuously stipitate, the stipe about as long as the involucre. Costa Rica to Colombia (Chocó); from 0 to 400 m in Caribbean and southwestern Costa Rica.

This species and *Trichomanes tuerckheimii* are noteworthy in having the laminae flatly appressed to the trunk of the supporting tree. *T. ankersii* is smaller, with a lacier appearance. It is not yet known from La Selva proper, but occurs on the Cloud Forest Ridge just off the southwestern boundary.

3. *Trichomanes collariatum* Bosch

*Rhizome* stout, appressed-climbing on trunks. *Petiole* 0–3(–8) cm long, terete, alate. *Laminae* lanceolate, 15–50 cm long, 4–16 cm broad, bipinnately divided. *Rachis* alate throughout. *Pinnae* 20–35 pairs, to 8.5 cm long, alternate. Southern Mexico to Brazil; widespread in Costa Rica from 0 to 1,500 m.

A common low-trunk epiphyte on small trees in the understory of primary forest, this is perhaps our most abundant *Trichomanes*.

4. *Trichomanes crispum* L.

Epiphyte, the *rhizome* stout, suberect. *Petiole* 1–8(–12) cm long, not alate but somewhat flattened, with spreading, brownish trichomes. *Lamina* narrowly lanceolate, (3.5–)5–26(–37) cm long, 1.5–4.7 cm wide, once-pinnate, pubescent especially along the veins, the *rachis* alate often nearly to the base. *Pinnae* 14–48 pairs below the pinnatifid apex, alternate to subopposite, to ca.

3 cm long and 0.8 cm wide, broadly attached to constricted at the base, the margins entire to obscurely sinuate. *Sori* 1–5 at apex of segments, the involucre uniformly green. Southern Mexico to Paraguay, West Indies; from 100 to 1,500 m in Costa Rica, mainly on the Caribbean slope but also on Cocos Island.

*Trichomanes crispum* is known from La Selva by a single collection (*Barcock A84, κ*), obtained from a canopy platform in the southern portion of the property. The label reads: "Epiphyte in full sun on tree trunk in canopy of Tropical Wet Forest. 100 ft. above ground. Completely shrivelled up in daytime." The species is probably more common, in such situations, than our records suggest.

5. *Trichomanes curtii* Rosenstock

Epiphyte, the *rhizome* creeping. *Petiole* 1–4 mm long, densely stellate-pubescent. *Lamina* ovate to roundish or obovate, 1–2 cm long, 0.7–1.5 cm wide, rounded or cuneate at the base, rounded apically, often irregularly lobed. *Venation* flabellate. *Sori* several to many, the indusial lips black-edged. Guatemala and Belize to Colombia; from 0 to 1,300 m in Costa Rica, on both coasts.

A tiny, inconspicuous and apparently uncommon understory trunk epiphyte in upland primary forest; it is easily confused in the field with the more common *T. godmanii*.

Lellinger (1989) attributes the very similar *T. punctatum* Poiré ssp. *labiatum* (Jenman) W. Boer to La Selva, but cites no material.

6. *Trichomanes diaphanum* Kunth

Creeping, usually epiphytic plants. *Petiole* 1.5–4 cm long, usually alate to the base. *Lamina* narrowly ovate in outline, translucent, tripinnately divided, 4–9 cm long and 1.5–4 cm broad. *Rachis* broadly alate. Indusial valves of *sori* plain green. Guatemala and Belize to Brazil, West Indies; ranging from 0 to 2,700 m in Costa Rica.

Fairly common at La Selva, especially along quebradas, where it occasionally grows on rocks as well as branches and twigs. *Trichomanes diaphanum* bears a superficial resemblance to some species of *Hymenophyllum*, and might also be confused with the more common *T. krausii*, which may occur in the same habitats and even on the same twig or rock.

7. *Trichomanes diversifrons* (Bory) Mett. ex Sadeb.

Terrestrial, the *rhizome* stout and erect. *Fronde* dimorphic. *Petiole* of sterile leaves 2–10 cm long, those of the fertile leaves 9–21 cm long. *Sterile lamina* lanceolate, deeply pinnatisect, 11–25 cm

long and 3.5–7 cm wide, the rachis often prolonged apically and rooting at the tip. *Pinnae* spreading, the margins serrulate. *Fertile lamina* simple, linear, (9–)19–25 cm long and 5–9 mm wide. *Sori* in a continuous line along each margin, completely immersed. Guatemala and Belize to Bolivia; widespread in Costa Rica, below 800 m, on both coasts.

Rare at La Selva, widely scattered in small populations in upland and alluvial primary forest.

#### 8. *Trichomanes ekmanii* W. Boer

Epiphyte, the *rhizome* creeping. *Petiole* short, 3–7 mm long, sparsely tomentose. *Lamina* obovate or oblong, 1.5–3 cm long, 0.5–1.5 cm wide, irregularly lobed especially in distal part. *Venation* pinnate, false veinlets numerous. *Sori* several, apically disposed. Belize to Bolivia, West Indies; from 0 to 1,200 m on the wetter parts of the Caribbean slope in Costa Rica.

Uncommon at La Selva in upland primary forest, where it grows among stilt roots or on trunk bases.

#### 9. *Trichomanes elegans* Rich.

Terrestrial, or occasionally epilithic, the *rhizome* erect or basally reclining. *Petioles* 7–24 cm long. *Lamina* firm and elastic, sea-green to deep blue-green in color, ovate to deltate, 9–27 cm long, 10–22 cm wide, finely 3–4-pinnate, the *rachis* winged. *Sori* deflexed, not visible from above. Nicaragua to Brazil, West Indies; from 0 to 800 m in Caribbean and southwestern Costa Rica.

At La Selva, this species has been accorded the informal name “plastic fern,” on account of its strikingly artificial appearance. Though conspicuous, it is not especially common. Growing usually along small creeks or seepages over basaltic rock in deep, upland, primary forest.

#### 10. *Trichomanes godmanii* Hook.

Epiphyte, the *rhizome* creeping. *Petiole* 4–10 mm long. *Lamina* reniform to orbicular or obovate, truncate to narrowed basally, 1–2.2 cm long and wide, the margin entire to slightly lobed. *Venation* pinnate basally, becoming flabellate distally, reticulate (with many transverse false veinlets); continuous submarginal vein present. *Sori* 1–several. Southern Mexico to Panama, Cuba; in Costa Rica, known only from the Caribbean slope and the Osa Peninsula, from 0 to 600 m.

Rather common at La Selva, where it is seen almost exclusively as a low trunk epiphyte on the ubiquitous palm, *Welfia georgii* H. A. Wendl.

ex Burret (or, much less frequently, on *Astrocaryum alatum* Loomis). It is, in addition, one of the few ferns ever seen in this habitat (*Elaphoglossum* sp. nov. is another). Putative specimens of *Trichomanes godmanii* collected from other substrates have always turned out to be *T. curtii* (see key for distinguishing characteristics). At Barro Colorado Island, where *Welfia* does not occur, *T. godmanii* is reported to grow on the palm *Scheelea zonensis* L. Bailey (Croat, 1978).

#### 11. *Trichomanes krausii* Hook. & Grev.

Creeping, epiphytic or epilithic fern. *Petiole* obsolete to 1.5 cm long, densely tomentose. *Lamina* oblong to ovate or obovate, 2–4 cm long, 1–2.5 cm wide, pinnatifid or bipinnatifid nearly to the rachis. Sinuses with stellate *trichomes*, the marginal trichomes simple or bifid; lower part of costa on underside of lamina tomentose (as petiole). Indusial valves of *sori* dark-edged. Central Mexico to Argentina; south Florida and the West Indies; widespread in Costa Rica from 0 to 1,500 m.

One of our more common *Trichomanes* species, growing on twigs or branches in cacao or primary upland or alluvial forest, or along creeks (where it may also grow on rocks). It is confused only with *T. diaphanum*, which has more finely divided laminae and glabrous (or at least not tomentose) petioles.

#### 12. *Trichomanes membranaceum* L.

Creeping epiphytes, or occasionally epilithic. *Petiole* obsolete to about 3 mm long, stout, densely tomentose. *Lamina* suborbicular to obovate, spatulate or ligulate, 1.5–5.2 cm long and to nearly as wide. *Margins* entire to irregularly lobed or incised, bearing paired, suborbicular scales (these frequently missing on old or damaged leaves). *Venation* flabellate. Indusial valves of *sori* uniformly green. Guatemala and Belize to Bolivia, West Indies; from 0 to 1,100 m in Costa Rica, on both slopes.

Of the “thalloid” *Trichomanes* species (i.e., those with small, simple fronds), this is perhaps our most common as well as our largest. Usually found growing on trunk bases or even on rocks in low, richly forested sites.

#### 13. *Trichomanes osmundoides* DC. ex Poirlet

Terrestrial, the *rhizome* generally short. *Fronde* dimorphic. *Petiole of sterile fronds* 0.5–5 cm long. *Sterile lamina* lanceolate, 5–17 cm long and 1.5–4 cm wide, deeply pinnatifid, the sinuses acute. *Lobes* numerous, about 1.5–4 mm wide, rounded or obtuse apically, the margins minutely sinuate to serrulate. *Petiole of fertile fronds* 3–12 cm long. *Fertile lamina* narrowly linear, 3.5–12 cm long



and 2–5 mm wide, the *sori* about 20–40 pairs, on either side of the narrowly winged rachis. Costa Rica to Colombia and Venezuela, West Indies; from below about 700 m in Caribbean and southwestern Costa Rica.

A distinctive, though seldom-collected, species. It is not yet known from La Selva proper, but has been collected from along the R. Peje just off the western boundary.

#### 14. *Trichomanes pinnatum* Hedwig

Terrestrial, the *rhizome* brief. *Fronde* monomorphic. *Petiole* terete, nonalate, 2.5–27 cm long (longest on fertile fronds). *Lamina* ovate to deltate, 6.5–25 cm long, 4–25 cm wide, pinnate, the rachis sometimes prolonged apically and rooting. *Pinnae* 4–16 pairs, 2–13 cm long, 0.6–2 cm wide, linear-lanceolate, sessile, the margins serrate. *False veinlets* numerous. *Sori* continuous along each pinna margin, conspicuously stipitate. Mexico to Bolivia, West Indies; a lowland species, from below 800 m in Caribbean and southwestern Costa Rica.

Very rare at La Selva, in upland primary forest in the vicinity of Plot III and along the South Boundary.

#### 15. *Trichomanes rigidum* Sw.

Terrestrial, the *rhizome* generally erect and to about 10 cm tall. *Fronde* monomorphic. *Petiole* 4–20 cm long. *Lamina* ovate to deltate, 5–23 cm long, 5–17 cm wide, finely 3–4-pinnate, the *rachis* largely terete. *Sori* not reflexed. Southern Mexico to Bolivia, West Indies; Old World tropics; widespread in Costa Rica from 50 to 2,100 m.

The only collection of this species from our area is Gómez 6742 (CR), from “La Selva, Sendero Esquinas.” Although *T. rigidum* has not been found at La Selva in recent years, the specimen is correctly identified and there is no compelling reason to suspect a label mixup. It should be sought in primary forest in the area indicated.

Though resembling *Trichomanes elegans* in general aspect, *T. rigidum* has more finely divided leaves and lacks the artificial appearance of the former species.

#### 16. *Trichomanes tuerckheimii* Christ

Epiphyte, the *rhizome* creeping. *Petiole* 1–3 mm long, terete. *Lamina* broadly oblong to lanceolate, usually dark green, pinnately divided, 2.5–19.5 cm long and 1.5–7 cm wide, truncate basally. *Rachis* and costae rusty-tomentose below. *Pinnae* 4–18 pairs, mostly 1–4.5 cm long and 0.4–1 cm broad, adnate to the rachis and spreading horizontally, the *margins* entire to

crenate. *Sori* short-stalked, the lips erect. Southern Mexico to Peru and Surinam; a lowland species, from below about 600 m in Caribbean and southwestern Costa Rica.

Like *T. ankersii*, this species grows with the laminae flattened against the trunk of the supporting tree. It is very rare at La Selva, known by only two collections from upland primary forest.

### 5. METAXYACEAE

TRYON, R. 1986. 12 C. Metaxyaceae. Pp. 13–16 in G. HARLING AND L. ANDERSSON, eds., Flora of Ecuador, No. 27. Univ. Göteborg, Stockholm.

Terrestrial plants with large, stout, prostrate *rhizome* covered with soft, golden-brown trichomes, completely lacking scales. *Lamina* large, once-pinnate, circinate in veneration, the *venation* free. *Sori* round, abaxial. *Sporangia* short-stalked, with the annulus just barely oblique.

Metaxyaceae is a monotypic, neotropical family. Though generally held to be related to the tree-ferns and sometimes included in the Cyatheaceae, it bears little resemblance to the members of that family at La Selva.

#### 1. METAXYA C. Presl

Characters of the family. The single species ranges from southern Mexico to Bolivia, and occurs sparingly in the West Indies.

##### 1. *Metaxya rostrata* (Kunth) C. Presl

*Petiole* 35–100 cm long, light brown, glabrous. *Lamina* lanceolate, 50–130 cm long, chartaceous, once-pinnate. *Pinnae* narrowly lanceolate, 11–19 pairs, 10–50 cm long and 1.8–4 cm wide, stalked, the *margins* entire (but serrate toward the apex). *Sori* round, borne close to the costa, lacking an indusium. A lowland species, from below 700 m in Caribbean and southwestern Costa Rica.

Very rare at La Selva, known only from the ridge to the west of Q. El Salto near Line 2700. It also occurs in the nearby Cerros Sardinal, Chilmate, where it abounds.

*Pinnae* on very small, juvenile plants are serrately lobed throughout. The adult plants bear a strong, superficial resemblance to *Thelypteris falcata*.

### 6. CYATHEACEAE

GOMEZ, L. D. 1983. Cyatheaceae and Dicksoniaceae. Pp. 225–228 in D. H. JANZEN, ed., Costa Rican natural history. University of Chicago Press, Chicago. 816 pp.

TRYON, R. 1970. The classification of the Cyatheaceae. Contr. Gray Herb. 200: 3–53.

———. 1986. 13. Cyatheaceae. Pp. 17–59 in G. HARLING AND L. ANDERSSON, eds., *Flora of Ecuador*, No. 27. Univ. Göteborg, Stockholm.

Mostly arborescent ferns, the *trunk* (in ours) about 0.5–12 m tall in fertile individuals (rarely obsolete). *Scales* present, at least on the petiole bases and croziers. *Petiole* and sometimes the frond axes spiny (rarely unarmed). *Lamina* monomorphic, mostly 3–4-pinnate (rarely less extensively divided or even, outside our area, simple), circinate in veneration, the *venation* always free in our species. *Sori* abaxial, round, indusiate or not. *Annulus* oblique.

Most La Selva “tree-fern” species are easily distinguished by their arborescent habit, spinose and scaly (at least basally) petioles and large, decomposed laminae. *Cyathea ursina*, however, diverges markedly in being acaulescent, lacking spines and having bipinnatifid laminae.

A pantropical family, comprising four genera and about 440 species as here construed. In addition to the two genera known from La Selva, *Cnemidaria* C. Presl also occurs in Costa Rica. At higher elevations, arborescent ferns belonging to the families Dicksoniaceae (with marginal sori) and Lophosoriaceae (lacking scales) may be encountered.

Collections accumulated over many years of intensive collecting do not substantiate the total of 16 species of Cyatheaceae attributed to La Selva by Gómez (1983).

#### KEY TO THE GENERA

1. Petiole scales with minute apical setae; petiole bases and unexpanded croziers with blackish, shiny spines which are rather easily broken off; sori conspicuously indusiate. . . . . 1. *ALSOPHILA*.
1. Petiole scales rounded to acute at the tip, without apical setae; petiole bases and unexpanded croziers spineless, or with paler, firmly attached spines; sori exindusiate, or the indusium delicate and inconspicuous. . . . . 2. *CYATHEA*.

#### 1. *ALSOPHILA* R. Br.

CONANT, D. S. 1983. A revision of the genus *Alsophila* (Cyatheaceae) in the Americas. *J. Arnold Arb.* 64: 333–382.

GASTONY, G. J. 1973. A revision of the fern genus *Nephelea*. *Contr. Gray Herb.* 203: 81–148.

Mostly tall, stately arborescent ferns, with large, decomposed laminae. *Scales* of the petiole base with dark, apical setae. *Spines* of the petiole bases and croziers in our species “corticinate” (derived from the cortical tissue of the petiole), blackish, hollow-based, superficial and rather easily pushed off. *Sori* exindusiate or (as in our species) with a conspicuous indusium.

A pantropical genus of about 230 species, only about 30 of which are neotropical. The latter

range from central Mexico to Uruguay, and throughout the West Indies. Five species occur in Costa Rica, all of which were formerly classed in *Nephelea* R. Tryon (Tryon, 1970; Gastony, 1973), an exclusively neotropical assemblage of 18 species. Conant (1983), however, includes *Nephelea* within the larger and older genus *Alsophila*, based on observations of rampant “intergeneric” hybridization and evidence that new species have arisen from such hybrids.

#### KEY TO THE SPECIES

1. Veins beneath moderately pubescent with blackish, stellate trichomes; petiole and rachis chocolate-brown (in life); larger pinnules generally more than 1.6 cm wide. . . . . 1. *A. cuspidata*.
1. Veins beneath sparsely pubescent with simple hairs; petiole and rachis reddish-brown; larger pinnules generally less than 1.6 cm wide. . . . . 2. *A. firma*.

1. ***Alsophila cuspidata*** (Kunze) Conant  
(=*Nephelea cuspidata* (Kunze) R. Tryon; *Cyathea punctifera* Christ)

*Stem* (at La Selva) about 2.5–7 m tall. *Petiole* to 0.5 m long. *Lamina* to 3 m long and 1.5 m wide, bipinnate-pinnatifid to nearly tripinnate. Larger *pinnules* mostly 8–12 cm long and 1.7–2.3 cm wide, the *ultimate segments* entire. *Rachis* dark brown. *Indusium* conspicuous, rupturing at maturity. Nicaragua to Paraguay; from 0 to 1,400 m in Caribbean and southwestern Costa Rica.

One of our more common large tree ferns, occurring widely in primary forest and old secondary forest. It is similar in stature and appearance to *Alsophila firma*, but can easily be distinguished in the field by its dark, chocolate-brown (rather than reddish-brown) rachis and petiole.

2. ***Alsophila firma*** (Baker) Conant  
(=*Nephelea mexicana* (Schldl. & Cham.) R. Tryon)

*Stem* (at La Selva) about 1.5–6 m tall. *Petiole* to 1.5 m long. *Lamina* about 2–3.2 m long, to 1.4 m wide, bipinnate-pinnatifid to tripinnate. *Rachis* reddish-brown. Larger *pinnules* mostly 5–12 cm long and 0.9–1.6 cm wide, the *ultimate segments* entire. *Indusium* conspicuous, though delicate and ultimately falling. Mexico to Ecuador; widespread in Costa Rica from about 0 to 1,300 m.

Similar in general appearance to *A. cuspidata*, this species is equally as common at La Selva, though perhaps more so in old secondary forest.

#### 2. *CYATHEA* J. E. Smith

BARRINGTON, D. S. 1978. A revision of *Trichipteris* (Cyatheaceae). *Contr. Gray Herb.* 208: 3–93.

- LELLINGER, D. B. 1987. The disposition of *Trichopteris* (Cyatheaceae). *Amer. Fern J.* 77: 90–94.
- RIBA, R. 1967. Revisión monográfica del complejo *Alsophila Swartziana* Martius (Cyatheaceae). *Anales Inst. Biol. Univ. Nac. México* 38, Sér. Bot. 1: 61–100.
- SMITH, A. R. AND M. H. GRAYUM. 1988. *Cyathea stolzei* × *ursina*, a distinctive tree fern hybrid from Costa Rica. *Amer. Fern J.* 78: 105–108.
- TRYON, R. 1976. A revision of the genus *Cyathea*. *Contr. Gray Herb.* 206: 19–98.

Terrestrial ferns, the *rhizome* erect and brief or, much more frequently, arborescent and to 10–12 m tall or more. *Lamina* once-pinnate to pinnate-pinnatifid or, most commonly, large and decompound. *Scales* of petiole base lacking apical setae. *Spines* of petiole bases and croziers non-corticate, rigid and firmly attached (rarely absent). *Sori* exindusiate or indusiate.

As treated here, *Cyathea* is a strictly neotropical genus of about 105 species, ranging from southern Mexico to northern Argentina and throughout the West Indies. The Costa Rican species number about 25. All of the La Selva species except *C. multiflora* have formerly been included in *Trichopteris* C. Presl (sometimes also spelled *Trichopteris*), distinguished from *Cyathea* s. str. merely by the absence of an indusium. We follow Lellinger (1987) in submerging the Costa Rican species of *Trichopteris* in *Cyathea*.

#### KEY TO THE SPECIES

1. *Lamina* merely pinnate-pinnatifid; plants lacking a distinct trunk at maturity, or the trunk less than 0.5 m tall; petiole bases lacking spines. . . . . 5. *C. ursina*.
1. *Lamina* 3–4-pinnate; plants at maturity with a trunk at least 0.5 m tall; petiole bases spiny.
  2. Rachises of pinnae conspicuously spiny; petiole scales less than 2.5 mm wide, pale or reddish-brown. . . . . 1. *C. microdonta*.
  2. Rachises of pinnae lacking spines; petiole scales more than 2.5 mm wide, medium to blackish-brown.
    3. Petiole and rachis pubescent with spreading hairs; laminar surface conspicuously pubescent above with whitish trichomes; petiole scales with narrow white margins bordered by a thin dark line. . . . . 4. *C. trichiata*.
    3. Petiole and rachis with minute, appressed indumentum; laminar surface glabrous above (the veins may bear trichomes); petiole scales not doubly margined.
      4. Laminar surface pubescent below; hairs on upper surface of rachises whitish; indusium present (though inconspicuous); common. . . . . 2. *C. multiflora*.
      4. Laminar surface glabrous below; hairs on upper surface of rachises dark brown; indusium lacking; rare. . . . . 3. *C. schiedeana*.

#### 1. *Cyathea microdonta* (Desv.) Domin (=*Trichopteris microdonta* (Desv.) R. Tryon)

*Stem* to about 2.5 m tall at La Selva (to 6 m elsewhere). *Petiole* 0.6–1.8 m long. *Lamina* 1–2.5 m long, bipinnate-pinnatifid. Largest *pinnules* to about 10 cm long and 2 cm wide, the *ultimate segments* entire to serrulate. Southern Mexico to southeastern Brazil, West Indies; widespread in Costa Rica from 0 to 1,400 m.

Occasional at La Selva, usually in disturbed sites in alluvial forest (near rivers and the lower parts of major quebradas); especially common along the Sendero El Atajo.

Though the plants may attain a respectable height, they often become fertile when the stem is only about 0.5 m tall. This is our most well-armed tree-fern; not only are the petiolar spines especially stout and sharp, but they extend onto the pinna-rachises as well.

#### 2. *Cyathea multiflora* J. E. Smith (=*Hemitelia multiflora* (J. E. Smith) R. Br.)

*Stem* 0.5–3(–5) m tall. *Petiole* 15–50 cm long. *Lamina* bipinnate-pinnatifid, to about 1.5 m long and 60–110 cm wide. Largest *pinnules* 4–8(–10) cm long and 1.1–2.2 cm wide, the *ultimate segments* subentire to serrate. *Indusium* rather inconspicuous, membranaceous and subtending the sorus from below. Guatemala to Bolivia; widespread in Costa Rica from sea level to about 1,800 m.

The most widespread and abundant tree-fern at La Selva, common throughout in primary forest. It seldom attains the stature of our species of *Alsophila*. Occasional slender-stemmed, fertile individuals with atypically small laminae (seen especially along the Camino Experimental) appear to be diseased.

#### 3. *Cyathea schiedeana* (C. Presl) Domin (=*Trichopteris schiedeana* (C. Presl) R. Tryon)

*Stem* to perhaps 2 m tall at La Selva (to 7 m elsewhere). *Petiole* 30–70 cm long. *Lamina* 1–2 m long, bipinnate-pinnatifid. Largest *pinnules* 6–11 cm long, 1–2 cm wide, the *ultimate segments* entire to obscurely and bluntly toothed. Southern Mexico to Panama; widespread in Costa Rica, from 0 to 2,000 m.

*Cyathea schiedeana* is known from but a single collection at La Selva, from the swamp at the headwaters of Q. Leonel.

#### 4. *Cyathea trichiata* (Maxon) Domin (=*Trichopteris trichiata* (Maxon) R. Tryon)

*Stem* to perhaps 10 m tall. *Fronks* to 3.5 m long. *Petioles* and rachis copiously pubescent, the

former ca 1.5 m long. *Lamina* bipinnate- to tri-pinnate-pinnatifid, to 2 m wide in the middle; both laminar surfaces pubescent. Largest *pinnales* 8–12.5 cm long and 1.1–2.3 cm wide, the *ultimate segments* crenate to serrately lobed. Costa Rica to Venezuela and Ecuador; from 0 to 1,200 m in Caribbean and southwestern Costa Rica.

Common at La Selva along the rivers and lower portions of major streams, becoming established in disturbed sites. Particularly large individuals occur in some shaded coves, such as near Rafael's House.

This is our tallest tree-fern, though it is more slender and graceful than the *Alsophila* species. It is easily distinguished from the other tree-ferns at La Selva, even in juvenile condition, by the abundant, whitish pubescence.

5. *Cyathea ursina* (Maxon) Lellinger  
(=*Trichipteris ursina* (Maxon) R. Tryon)

*Stem* very short, to perhaps 15 cm long but usually much shorter. *Petiole* about 15–25 cm long, this and the rachis densely covered with spreading brown scales. *Rachis* winged toward apex. *Lamina* about 60–110 cm long and 20–30 cm wide, lanceolate, pinnate-pinnatifid, tapered to a pinnatifid apex, the basal pinnae much reduced. Largest *pinnae* 7–19 cm long, 2.5–3.5 cm wide, the *ultimate segments* entire or obscurely toothed. Caribbean lowlands of Belize, Nicaragua, Costa Rica and Panama; in Costa Rica, known only from below 100 m in the Sarapiquí region.

*Cyathea ursina* is one of our most attractive ferns. It appears restricted to primary swamp forests, such as in Plots I and II, where it may be locally common.

This is not a "tree-fern" in any layman's sense of the term; it more closely resembles a rather large, copiously scaly member of *Thelypteris* subgenus *Goniopteris* than any of our other species of *Cyathea*. In the Cerros Sardinal near Chilamate, *C. ursina* hybridizes with the even more reduced *Cyathea stolzei* A. R. Smith ex Lellinger (Smith & Grayum, 1988).

## 7. POLYPODIACEAE

STOLZE, R. G. 1981. Ferns and fern allies of Guatemala. Part II. Polyodiaceae. *Fieldiana, Bot. n.s.* 6: 1–522.

Plants terrestrial, epiphytic or even aquatic, the *rhizome* erect and obsolescent to subarborescent, or long- to short-creeping. *Lamina* circinate in bud, mono- or dimorphic, simple and entire to decompound, the *venation* free to reticulate. *Sporangia* usually arranged in discrete abaxial or marginal sori, occasionally borne individually along the veins or covering the abaxial surface of the fertile fronds or segments. *Annulus* vertical, interrupted by the sporangial stalk. *Sori* round to elliptic or linear, indusiate or not.

The family Polypodiaceae, as here construed, includes the majority of living ferns and is, therefore, extraordinarily variable. Perhaps the only single character distinguishing this family from all of the foregoing ones is the universal presence of a vertical annulus (interrupted by the stalk of the sporangium). Since this character hardly lends itself to field identification, the best course is to learn the remaining families, which for the most part are rather distinctive, and the Polypodiaceae will fall out by elimination. Among La Selvan ferns, only the non-polypodiaceous *Metaxya rostrata* (Metaxyaceae) and *Cyathea ursina* (Cyatheaceae) may cause problems, and these have been included in the following key.

The present treatment of the Polypodiaceae as a huge, all-encompassing family follows that of Croat (1978) and Stolze (1981), among others. So interpreted, the family is a cosmopolitan one, containing (by Stolze's estimate) 150–180 genera and 6,000–10,000 species. About 67–80 genera (depending on the concepts adopted) and 675 species are known from Costa Rica.

Although there have been many attempts to divide up Polypodiaceae s.l., none have met with wide acceptance, and no consensus has emerged among pteridologists regarding either the number of segregate families to be recognized or their circumscriptions.

### KEY TO THE GENERA

1. Stipe, rachis and often the costae conspicuously spiny; lamina 3-pinnate-pinnatifid to 4-pinnate; rhizome long-creeping; sori marginal. . . . . 12. *HYPOLEPIS*.
1. Rachis and costae never spiny (very rarely, the base of the stipe may be).
  2. Plants terrestrial, high-climbing by means of the elongated rachis and petiole; sori linear, parallel to the costae. . . . . 31. *SALPICHLAENA*.
  2. Plants not climbing or, if so, by means of the elongated rhizome rather than the frond axes.
    3. Fronds markedly dimorphic, the fertile laminae somewhat to considerably smaller, achlorophyllous and completely carpeted abaxially with sporangia.

4. Sterile (and fertile) lamina simple, entire. . . . . 13. *ELAPHOGLOSSUM*.
4. Sterile lamina variously compound.
5. Sterile lamina 5–6 times dichotomously divided into linear lobes; fertile lamina more or less circular, simple; tiny ferns, the fronds less than 15 cm long. . . . . 13. *ELAPHOGLOSSUM*.
5. Sterile lamina pinnately compound; fertile lamina also pinnately divided; larger ferns, the fronds more than 15 cm long.
6. Sterile lamina bipinnate-pinnatifid to tripinnate. . . . . 26. *POLYBOTRYA*.
6. Sterile lamina pinnate to pinnate-pinnatifid.
7. Venation reticulate. . . . . 6. *BOLBITIS*.
7. Venation free, with the veins numerous and closely parallel.
8. Fertile lamina pinnate-pinnatifid; pinnae not articulate to the rachis; short-stemmed plants usually on rotting logs. . . . . 26. *POLYBOTRYA*.
8. Fertile lamina simply pinnate; pinnae articulate to the rachis; appressed-climbing trunk epiphytes. . . . . 21. *LOMARIOPSIS*.
3. Fronds not dimorphic or, if slightly so, always chlorophyllous and with the sporangia in discrete sori or else distributed only along the veins.
9. Sporangia borne individually along the veins, not arranged in discrete sori.
10. Lamina bipinnately compound, green above, strongly whitened beneath; weedy plants. . . . . 25. *PITYROGRAMMA*.
10. Lamina simple, not bicolored.
11. Lamina palmately veined and lobed, the rhizome erect; weedy plants, terrestrial or on rotting logs. . . . . 17. *HEMIONITIS*.
11. Lamina pinnately veined, entire, the rhizome long-creeping; epiphytic in primary forest. . . . . 2. *ANETIUM*.
9. Sporangia densely aggregated into discrete sori, these sometimes following the veins.
12. Sporangia borne in marginal or submarginal, subglobose, pouch-like involucre opening outward or downward; lamina bipinnate-pinnatifid to 3–4-pinnate.
13. Rhizome erect, scaly; indusium strictly abaxial, flat, the adaxial side of the involucre formed by the laminar tissue. . . . . 30. *SACCOLOMA*.
13. Rhizome short- to long-creeping, glabrous or hairy, lacking scales; indusium cup- or purse-shaped, recurved, forming the entire involucre. . . . . 9. *DENNSTAEDTIA*.
12. Sori abaxial or, if marginal, elongate or linear—never subglobose and pouch-like.
14. Sori marginal and elongate to linear, the long axis parallel to the laminar margin.
15. Lamina simple, dichotomously or subdichotomously deeply divided into few long, lance-attenuate lobes, these fertile only in the apical portions; epiphytic. . . . . 10. *DICRANOGLOSSUM*.
15. Lamina compound or, if simple, then entire or with very few remote lobes; never dichotomously lobed or divided.
16. Lamina simple, linear or narrowly lanceolate, the margins entire or rarely with very few remote teeth or lobes. . . . . 35. *VITTARIA*.
16. Lamina compound.
17. Lamina once-pinnate or, if bipinnate, the pinnules entire to serrate.
18. Sporangia covered by (and borne on) the reflexed margin of the lamina; both margins of each pinnule typically fertile, the sterile tips serrate. . . . . 1. *ADIANTUM*.
18. Sporangia covered by a separate indusium, opening toward the margin; only the anterior margins of the pinnules fertile, the sterile margins entire. . . . . 20. *LINDSAEA*.
17. Lamina at least partly bipinnate-pinnatifid, the basal pinnae bearing free pinnules which are themselves deeply lobed.
19. Rhizome pubescent, lacking scales; stipe and rachis conspicuously pubescent with whitish trichomes; venation free. . . . . 22. *LONCHITIS*.
19. Rhizome scaly; stipe and rachis glabrous, or with minute and scattered hairs; venation reticulate or free. . . . . 29. *PTERIS*.
14. Sori not marginal or, if so, then rounded or else elongate with the long axis perpendicular to the laminar margin.
20. Lamina fully bipinnate to 3–4-pinnate, to well above the middle.
21. Sori elliptical to linear.
22. Fronds exactly bipinnate, the pinnules entire; sori elliptical; terrestrial plants. . . . . 11. *DIDYMOCHLAENA*.
22. Fronds bipinnate with the pinnules toothed or lobed, to essentially tripinnate; sori linear; terrestrial or epiphytic plants.
23. Epiphytic ferns, the fronds less than 50 cm long; pinnules usually merely toothed (or the basal ones with a few lobes). . . . . 4. *ASPLENIUM*.
23. Terrestrial ferns, the fronds more than 50 cm long; pinnules usually

- pinnatifid to pinnately lobed (i.e., the lamina virtually tripinnatifid).  
 ..... 12. *DIPLAZIUM*.
21. Sori round.
24. Basal posterior lobes of the basal pinnae much enlarged, at least twice as long as the basal anterior lobes; rachis pubescent all around, and sometimes scaly as well; stipe not glaucous.
25. Scales, as well as pubescence, present throughout the petiole and also on the rachis and costae; those at the base of the stipe dense, hairlike, more than 1 cm long; frond axes not sulcate above or, if so, the sulci not flanked by decurrent ridges. .... 7. *CTENITIS*.
25. Scales restricted to the basal half of the petiole, sparse, less than 1 cm long; frond axes sulcate above, the sulci flanked by ridges decurrent on the axis of the next lower order. .... 19. *LASTREOPSIS*.
24. Basal posterior lobes of the basal pinnae not so enlarged; rachis essentially glabrous, at least beneath; petiole conspicuously glaucous toward the base. .... 34. *THELYPTERIS*.
20. Lamina simple to pinnate-pinnatifid, or bipinnate only in the basal half.
26. Sori oblong or elliptical to linear.
27. Tiny epiphytic ferns, the largest fertile fronds (including stipe) less than 10 cm long; sori linear, exindusiate.
28. Lamina Y-shaped to 2–3 times dichotomously lobed; fronds minute, less than 2 cm long. .... 15. *HECISTOPTERIS*.
28. Lamina simple or divided, but never dichotomously, at least the fertile ones more than 2 cm long.
29. Lamina linear, 4 mm wide or less, entire to deeply serrate, monomorphic; sori linear, exindusiate, one per frond in central groove. .... 14. *GRAMMITIS*.
29. Lamina more than 4 mm wide, pinnately lobed to virtually pinnate, slightly dimorphic (the sterile fronds 1–4-lobed, the fertile 3–15-lobed); sori elliptical, indusiate, one per pinna. 4. *ASPENIUM*.
27. Larger ferns, the largest fertile fronds more than 10 cm long.
30. Sori exindusiate; venation reticulate; lamina simple and entire to pinnate (in which case the sori are oblong to elliptical, or else linear and reticulately following the veins).
31. Lamina pinnate to pinnate-pinnatifid or, rarely, simple (in which case the rhizome is erect or short-creeping, and the sterile fronds have petioles more than 25 cm long); sori oblong to elliptical; terrestrial, or on rocks, logs, etc. .... 34. *THELYPTERIS*.
31. Lamina simple and entire, or with few basal or remote lobes; rhizome long-creeping, the sterile fronds with petioles less than 25 cm long, or else fronds without definite petioles; sori linear, more or less reticulately following the veins; epiphytic.
32. Areolae without free included veinlets; rhizome short-creeping; fronds without definite petioles. .... 3. *ANTROPHYUM*.
32. Areolae with free included veinlets; rhizome long-creeping; fronds with obvious petioles. .... 28. *PSEUDOCOLYSIS*.
30. Sori indusiate; venation free, or very rarely reticulate at the margin; leaves bipinnatifid, pinnate or deeply pinnately lobed, rarely simple and entire (the sori then linear, but not reticulately arranged).
33. Lamina simple; rosette-forming epiphytes. .... 4. *ASPENIUM*.
33. Lamina bipinnatifid, pinnate or deeply pinnately lobed; plants terrestrial or epiphytic, but not forming rosettes.
34. Pinnae or lobes entire, each bearing two sori, these with the long axis running parallel to the midvein on either side; fronds slightly dimorphic, the fertile pinnae longer and narrower; plants terrestrial. .... 5. *BLECHNUM*.
34. Pinnae entire to crenate, serrate or pinnately lobed, each generally bearing more than 2 sori, these oblique or perpendicular to the midvein; fronds not at all dimorphic; plants terrestrial or epiphytic.
35. Pinnae opposite or very nearly so, entire, sessile and cordate-clasping at the base; venation reticulate toward the margin; large terrestrial fern; very rare. .... 16. *HEMIDICTYUM*.
35. Pinnae alternate, entire to serrate or lobed, at least the

- basal ones usually stalked; venation free; terrestrial or epiphytic; common.
36. Rhizome scales clathrate (the cells dark around the edges, clear in the center); sori usually always borne singly; plants at La Selva epiphytic to epilithic or on rotting logs, rarely terrestrial. . . . 4. *ASPLENIUM*.
36. Rhizome scales not clathrate, the cells uniformly brownish; at least some sori (usually on the larger lobes of the basal pinnae) borne in back-to-back pairs; plants at La Selva strictly terrestrial. . . . 12. *DIPLAZIUM*.
26. Sori round.
37. Lamina simple and entire; venation free, the veins numerous and closely parallel; sori indusiate; petiole conspicuously articulate below the middle. . . . 24. *OLEANDRA*.
37. Lamina not both simple and entire (or, if so, the sori exindusiate and the venation reticulate); petiole not articulate, or articulate at the very base, where it meets the rhizome.
38. Lamina pinnate, long and narrow, the pinnae more than 40 pairs and articulate with the rachis; venation open; sori indusiate; rhizome erect.
39. Sori in 2 rows between the costa and the pinna margin; pinna margins entire, or very obscurely toothed; terrestrial. . . . 8. *CYCLOPELTIS*.
39. Sori in 1 row between the costa and the pinna margin; pinna margins crenate to biserrate, at least apically; epiphytic or occasionally terrestrial. . . . 23. *NEPHROLEPIS*.
38. Lamina simple or with fewer than 40 pairs of free pinnae (or, if more, the sori exindusiate); pinnae never articulate with the rachis; venation open or areolate.
40. Lamina simple and entire, or palmately lobed.
41. Lamina palmately lobed or, if entire, with the petiole conspicuously scaly; plants epilithic or terrestrial; rare. . . . 33. *TECTARIA*.
41. Lamina simple, the petiole not obviously scaly; plants epiphytic; common. . . . 27. *POLYPODIUM*.
40. Lamina simple and pinnately lobed to pinnate-pinnatifid.
42. Plants terrestrial, with a stout, prostrate stem densely clothed with soft, golden-brown trichomes (especially apically); pinnae entire (except at tip); venation free, the veins numerous and closely parallel; sori mostly borne closer to costa than to margin; very rare. . . . *METAXYA* (see *METAXYACEAE*).
42. Plants, if terrestrial, lacking a stout, trichome-covered stem; pinnae and venation various, but the veins usually areolate and rarely closely parallel; some sori generally borne closer to the margin.
43. Pinna margins always entire (i.e., the lamina never more than once-pinnate); pinnae more or less broadly attached, never with true, terete stalks; plants terrestrial or epiphytic.
44. Petiole articulate with the rhizome (this not easily seen); venation free or reticulate; plants always epiphytic at La Selva. . . . 27. *POLYPODIUM*.
44. Petiole not articulate with the rhizome; venation conspicuously reticulate; coarse, terrestrial plants with creeping rhizomes. . . . 33. *TECTARIA*.
43. Pinna margins subentire to deeply lobed (i.e., the lamina subbipinnatifid to virtually bipinnate), or with a prominent basal lobe; at least the basal pinnae with true, terete stalks (except in *Tectaria brauniana*), however short; plants always terrestrial (or on rocks, rotting logs, etc.) at La Selva.
45. Basal pinnae each with a basal posterior lobe ca. 1/2 as long as the pinna itself; or, some of the basal pinnae (on some fronds) again pinnate, with at least one pair of completely free pinnules. . . . 33. *TECTARIA*.
45. Basal pinnae lacking enlarged basal posterior lobes; no pinnae again truly pinnate.
46. Petiole, rachis and croziers densely clothed with

- spreading, lustrous dark brown scales to more than 1.5 cm long; fronds lanceolate in outline; occasional, in swamp forest. . . . . *CYATHEA* (see *CYATHEACEAE*).
46. Petioles, etc., scaleless, or with scales few and remote and/or much less than 1.5 cm long; frond outline various.
47. Veins ending before the margin in narrowly clavate hydathodes; laminar tissue with microscopic, internal, pellucid glands (visible by transmitted light with a hand lens); laminar surface lacking trichomes; rachis with remote yet conspicuous lax, brown scales; indusium lacking; very rare, in swamp forest or along creeks. . . . . 32. *STIGMATOPTERIS*.
47. Veins running to the margin; laminar tissue lacking internal, pellucid glands; laminar surface bearing trichomes, these sometimes stellate and minute; rachis lacking conspicuous scales; sori with or without indusium; common, in many habitats. . . . . 34. *THELYPTERIS*.

### 1. ADIANTUM L.

- SCAMMAN, E. 1960. The maidenhair ferns (*Adiantum*) of Costa Rica. *Contr. Gray Herb.* 187: 3–22.
- SEYMOUR, F. C. 1975. *Adiantum* in Nicaragua. *Phytologia* 31: 1–15.

Terrestrial ferns, the *rhizome* usually long- or short-creeping. *Petioles* mostly slender, dark and lustrous. *Fronde*s monomorphic, pinnate to bipinnate in ours, the *ultimate segments* entire to serrate and usually “dimidiate” (i.e., attached at one side, thus looking like one half of a bilobed structure). *Venation* free, or occasionally reticulate. *Sori* elongate, marginal, the *indusium* (recurved laminar margin) opening away from the margin.

A cosmopolitan genus of 150–200 species, best represented in the tropics. About 27 species have been collected in Costa Rica.

*Adiantum* may usually be recognized at once by the distinctive and familiar dimidiate shape of the ultimate segments (at La Selva, only *A. seemannii* has non-dimidiate segments). Only two other genera at La Selva share this feature: *Didymochlaena*, with an erect stem and elliptical sori perpendicular to the margin, and the even more similar *Lindsaea*.

#### KEY TO THE SPECIES

1. Lamina once-pinnate, rarely with the lowermost pair of pinnae again pinnate (in which case the leaves are glaucous below).
  2. Pinnae with one continuous sorus along each edge; pinnae usually more than 2 cm wide and more than 5 cm long; very rare.
  3. Pinnae opposite, or very nearly so, subsessile or with a stalk to ca. 1 mm long; venation free; rachis glabrous; rhizome stout, short-creeping, the scales obvious, spreading. . . . . 2. *A. macrophyllum*.
3. Pinnae alternate, with a short stalk 1–5 mm long; rachis pubescent; venation partly reticulate; rhizome slender, long-creeping, the scales small, appressed. . . . . 7. *A. wilsonii*.
2. Pinnae with several short sori along each margin; pinnae alternate.
  4. Pinnae long-stalked, the stalks more than 1 cm long; pinnae ovate, mostly more than 2 cm wide and more than 5 cm long; very rare. . . . . 5. *A. seemannii*.
  4. Pinnae subsessile or short-stalked, the stalks much less than 1 cm long; pinnae usually less than 2 cm wide and less than 5 cm long; common plants.
    5. Pinnae lustrous below, green; margins of the sterile pinnae biserrate. . . . . 3. *A. obliquum*.
    5. Pinnae glaucous below; margins of the sterile pinnae finely serrulate. . . . . 4. *A. petiolatum*.
1. Lamina fully bipinnate, very rarely with only the lowermost pinnae again pinnate (in which case the leaves are green below).
  6. Lamina glaucous beneath; pinnules nearest the terminal segment not much reduced, at least half as long as the longest pinnules; rhizome very long-creeping, the petioles widely separated. . . . . 1. *A. latifolium*.
  6. Lamina green beneath; pinnules nearest the terminal segment much reduced, less than half as long as the longest pinnules; rhizome short-creeping, the petioles more approximate.
    7. Pinnate pinnae 4–12; pinnules fertile only on the anterior and distal margins. . . . . 6. *A. tetraphyllum*.
    7. Pinnate pinnae 0–5; at least some pinnules fertile on the posterior margins as well. . . . . 3. *A. obliquum*.



1. *Adiantum latifolium* Lam.

*Rhizome* long-creeping. *Petiole* 15–42 cm long, glossy and blackish, scurfy. *Lamina* 20–33 cm long, bipinnate, the pinnae 2–4 pairs. *Pinnules* glaucous below, the larger ones 1.7–5 cm long and 0.5–1.5 cm wide; sterile pinnules generally broadest, with finely serrate margins. *Sori* short, 6–12 on anterior margin, 3–6 on posterior margin. Southern Mexico to Paraguay, West Indies; from 0 to 1,200 m in Costa Rica, more common on the Caribbean slope.

This and *A. petiolatum* are our commonest weedy *Adiantum* species, occurring together in such habitats as the pejibaye clearing and disturbed slopes along the rivers.

2. *Adiantum macrophyllum* Sw.

*Rhizome* short-creeping. *Petiole* 12–46 cm long, glossy and blackish, glabrous. *Lamina* 14–29 cm long, once-pinnate, the pinnae 3–7 pairs, glaucous below, subsessile, opposite or nearly so, 4–10 cm long and 1.5–6.1 cm broad, somewhat deltate, broadly cuneate to truncate basally. *Rachis* glabrous. *Sori* long, one along each margin. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica, from 0 to 1,400 m.

Very rare at La Selva, known from one small population in a shaded cove along the R. Puerto Viejo at Rafael's Point.

3. *Adiantum obliquum* Willd.

*Rhizome* short-creeping. *Petiole* 9–40 cm long, glossy and blackish, more or less pubescent. *Lamina* 11–25 cm long, once-pinnate or (more commonly at La Selva) bipinnate at least at the base. *Pinnae* 8–16 pairs, the larger ones 2.5–7 cm long, 0.8–2.5 cm wide. Largest *ultimate segments* 2.3–5(–7) cm long, 0.7–1.5(–2.5) cm wide, dark to bright green on both surfaces (not glaucous), subsessile, the sterile ones marginally serrate. *Sori* short, numerous, borne along both margins. Southern Mexico to Bolivia, West Indies; from 0 to 900 m in Costa Rica, most common on the Caribbean slope.

A common and somewhat weedy fern, though generally restricted to disturbed areas in primary forest (such as along trails and at the edges of light gaps). *A. obliquum* may occasionally turn up in secondary areas or clearings, but not to the extent of *A. latifolium* or *A. petiolatum*. The latter is very similar to *A. obliquum*, differing in its more usually once-pinnate fronds and glaucous lower leaf surfaces.

4. *Adiantum petiolatum* Desv.

*Rhizome* short- to long-creeping. *Petiole* 9–25 cm long, black and glossy. *Lamina* 9–22 cm long, once-pinnate (rarely with the basal pinnae again pinnate), the pinnae 4–12 pairs. *Pinnae* 2.5–8 cm long, 1–3 cm wide, alternate, subsessile, glaucous below, the sterile ones finely serrulate marginally. *Sori* short, numerous, borne along both margins. Southern Mexico to Bolivia, West Indies; from 0 to 800 m in Costa Rica, on both slopes.

A common, weedy species in open, disturbed habitats at La Selva, often in association with *Adiantum latifolium*.

5. *Adiantum seemannii* Hook.

*Rhizome* short-creeping. *Petiole* 12–57 cm long, glossy and blackish, glabrous. *Lamina* 17–33 cm long, once-pinnate or (especially the fertile fronds) bipinnate basally, the pinnae 2–5 pairs. *Ultimate segments* 3.5–11 cm long, 1.2–8.5 cm wide, with long (1–4.5 cm) stalks, alternate, ovate, rounded to broadly cuneate basally, the sterile margins serrate. *Sori* numerous, borne along each margin. Southern Mexico to Colombia; widespread in Costa Rica, from 0 to 800 m.

*Adiantum seemannii* is very rare at La Selva, being known from a single population along the R. Puerto Viejo, upstream from the Q. Experimental.

6. *Adiantum tetraphyllum* Humb. & Bonpl. ex Willd.

(=*A. fructuosum* Sprengel)

*Rhizome* long- or short-creeping. *Petiole* 16–64 cm long, glossy and blackish, this and the rachis scurfy. *Lamina* 21–55 cm long, bipinnate with 2–8 pairs of pinnae. *Pinnules* subsessile, green on both sides, the larger ones 0.9–4.3 cm long and 3–10 mm wide, the sterile ones coarsely crenate-serrate marginally. *Sori* numerous, mostly along the anterior margin, a few apical. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica from 0 to 1,500 m.

Occasional at La Selva in relatively undisturbed alluvial forest (as in Discovery Woods) and in primary swamp forest (Plot II).

*Adiantum tetraphyllum* and *A. fructuosum* are supposed to differ in the nature of the rhizome (short- vs. long-creeping) and the orientation of the sterile apex of fertile pinnules; however, these characters vary independently at La Selva.

7. *Adiantum wilsonii* Hook.

*Rhizome* long-creeping. *Petiole* 17–23 cm long, glossy and blackish, somewhat pubescent. *Lam-*

*ina* 7–15 cm long, once-pinnate, with 1–3 pairs of pinnae. *Pinnae* short-stalked, alternate, 6–15 cm long and 1.5–5 cm wide, somewhat curved, green on both surfaces, the sterile ones serrate marginally. *Sori* long, continuous, one on each margin. Southern Mexico to Panama; from 0 to 900 m in Costa Rica, mostly on the Caribbean coast.

Very rare at La Selva, known from a single population near the mouth of the Q. El Salto.

## 2. ANETIUM (Kunze) Splitg.

Small trunk epiphytes with long-creeping *rhizome*. *Fronde* monomorphic, the lamina simple, entire and thickish. *Sporangia* scattered in small groups abaxially, mainly along the anastomosing veins.

A monotypic, neotropical genus, ranging from Chiapas to southeastern Brazil and throughout the West Indies.

### 1. *Anetium citrifolium* (L.) Splitg.

*Petioles* very brief or obsolete. *Fronde* limply pendent, the lamina generally 15–30 cm long, 2–8 cm wide, elliptic to oblanceolate. *Venation* copiously reticulate. *Indusium* lacking. From 0 to 800 m in the Caribbean lowlands and southwestern Costa Rica.

An occasional low trunk epiphyte, usually on fairly large trees, in primary forest.

## 3. ANTROPHYUM Kaulf.

BENEDICT, R. C. 1907. The genus *Antrophyum*—I. Synopsis of subgenera, and the American species. Bull. Torrey Bot. Club 34: 445–458.

Ours trunk epiphytes with short-creeping *rhizome*. *Fronde* monomorphic, the lamina simple, oblanceolate and entire. *Sori* abaxial, exindusiate and elongate, oblique or following the anastomosing veins.

*Antrophyum* is closely related to and most easily confused with *Vittaria* which, however, has strictly marginal sori. All but one of the neotropical species are occasionally segregated into their own genus, *Polytaenium* Desv. (distinguished solely by the absence of soral paraphyses).

As here treated, *Antrophyum* is pantropical and comprises perhaps 40 species. About 10 of these are neotropical, ranging from central Mexico south to Uruguay and throughout the West Indies. Six species occur in Costa Rica.

## KEY TO THE SPECIES

1. Lamina thick, the margins revolute, obtuse to acute or short-attenuate apically, broadest above the middle, the largest ones more than 2.5 cm wide; long axes of areolae running diagonal to the midvein. . . . . 1. *A. cajenense*.
1. Lamina thinner, the margins plane, long-attenuate apically, broadest near the middle, the largest ones less than 2.5 cm wide; axes of the areolae running nearly parallel to the midvein. 2. *A. lanceolatum*.

### 1. *Antrophyum cajenense* (Desv.) Sprengel (=*Polytaenium cajenense* (Desv.) Benedict)

*Lamina* spatulate or oblanceolate, long-attenuate at base, 12–40 cm long, 2–4.5 cm wide, sessile and closely approximate. *Margins* usually somewhat revolute. *Veins* obscure. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica from 0 to 1,400 m.

An occasional trunk epiphyte at La Selva, mainly in upland primary forest.

### 2. *Antrophyum lanceolatum* (L.) Kaulf. (=*Polytaenium feei* (Schaffner ex Fée) Maxon)

*Lamina* narrowly lanceolate, attenuate at base, 6–32 cm long, 0.8–2.0 cm wide, subsessile. *Margin* generally plane. *Venation* obscure. Southern Mexico to Brazil, West Indies; widespread in Costa Rica, from 0 to 1,500 m.

Occasional trunk epiphyte throughout, especially along creeks and in alluvial forest; abundant in cacao.

N.B.: In addition to the two species treated above, *Antrophyum lineatum* (Sw.) Kaulf. is vouchered for La Selva, by Gómez 981 (CR). Although this specimen is correctly identified, a label mixup is strongly indicated. The label reads, “abunda en lugares expuestos de la selva húmeda,” a statement suspiciously at odds with the fact that intensive collecting during the past ten years has failed to turn up a single additional specimen. Furthermore, no other Costa Rican collections of *A. lineatum* have been seen from below about 600 m elevation.

*Antrophyum lineatum* is easily recognized by its long, straight, closely parallel soral lines, running parallel with the midvein.

## 4. ASPLENIUM L.

MORTON, C. V. AND D. B. LELLINGER. 1966. The Polypodiaceae subfamily Asplenoideae in Venezuela. Mem. N.Y. Bot. Gard. 15: 1–49.

STOLZE, R. G. 1986. 14(6). Polypodiaceae—Asplenoideae. Pp. 1–83 in G. HARLING AND B. SPARRE, eds., Flora of Ecuador, No. 23. Univ. Göteborg, Stockholm.

Usually epiphytic or epilithic, occasionally terrestrial ferns, the *rhizome* usually obsolete or short- to rarely long-creeping (*A. holophlebium*). *Lamina* essentially monomorphic, simple (*A. serratum*) to pinnatifid, or more commonly, pinnate or bipinnatifid, rarely (in ours) bipinnate (*A. cuspidatum*). *Venation* generally free. *Sori* elongate to linear, indusiate, almost always borne singly.

A cosmopolitan genus of about 650 species, 45–50 of which occur in Costa Rica. It may be

easily confused with *Diplazium*, sometimes considered a near relative. Fortunately, at La Selva, *Asplenium* is nearly always epiphytic or epilithic, whereas all our species of *Diplazium* are strictly terrestrial. In addition, *Diplazium* usually has at least some paired sori. Technically, the two genera are distinguished by the nature of the rhizome scales (see generic key) and by their different chromosome numbers. *Asplenium* might also be confused with *Hemidictyum*.

#### KEY TO THE SPECIES

1. Lamina simple, entire or merely serrate; rosette-forming epiphytes. . . . . 11. *A. serratum*.
1. Lamina pinnatifid to more usually pinnate; plants often epiphytic, but never rosette-forming.
  2. Rhizome long-creeping; fronds very small, less than 5 cm long (including petiole), somewhat dimorphic, the sterile pinnae 1–4 pairs, the fertile ones 3–15 pairs; margins of pinnae entire. . . . . 6. *A. holophlebium*.
  2. Rhizome erect to short-creeping; fronds more than 5 cm long, never dimorphic; pinnae usually more than 9 pairs, the margins crenate to serrate, rarely entire.
    3. Rachis prolonged beyond the terminal pinnae, naked, whiplike and often budding or rooting apically; plants growing on rotting logs (rarely epilithic). . . . . 2. *A. cirrhatum*.
    3. Rachis not prolonged apically; plants epiphytic or epilithic.
      4. Petiole very short or almost lacking, usually less than 4 cm long, less than ¼ as long as the lamina; pinnae gradually reduced basally, the lowermost less than ½ as long as the longest; fronds usually less than 3.5 cm wide.
        5. Pinna margins deeply incised; petiole and rachis purplish-black, lustrous; sori 1–3 per pinna; occasional. . . . . 5. *A. formosum*.
        5. Pinna margins crenate; petiole and rachis green, dull; sori 3–9 per pinna; very rare. . . . . 8. *A. pteropus*.
      4. Petiole usually more than 4 cm long and more than ¼ as long as the lamina; lowermost pinnae more than ½ as long as longest pinnae; frond usually more than 3.5 cm wide.
        6. Plants epiphytic, on trunks or branches.
          7. Lamina fully bipinnate. . . . . 3. *A. cuspidatum*.
          7. Lamina simply pinnate to bipinnatifid, or, at best, the proximal pinnae with one free basal pinnule.
            8. Lamina terminating in a pinnatifid apex; pinnae (at least the basal ones) usually with a more or less pronounced basal anterior lobe, tooth or auricle; small plants, the fronds usually less than 11 cm wide; pinnae usually less than 1 cm wide. . . . . 3. *A. cuspidatum*.
            8. Lamina terminating in a pinna resembling the lateral pinnae; pinnae lacking a basal anterior tooth or auricle; larger plants, the fronds usually more than 11 cm wide; pinnae more than 1 cm wide.
              9. Pinna margins sharply serrate; petiole and rachis purplish-black, scaly. . . . . 10. *A. serra*.
              9. Pinna margins entire or obscurely crenulate; petiole and rachis dull gray-brown, lacking scales. . . . . 4. *A. falcinellum*.
    6. Plants epilithic, growing on rocks in fast-moving streams (rarely, terrestrial on streambanks).
      10. Rhizome short-creeping; pinnae subentire to shallowly crenate or serrate; largest sori to over 8 mm long. . . . . 9. *A. repandulum*.
      10. Rhizome erect; pinnae regularly deeply serrate; largest sori less than 8 mm long.
        11. Serrate portion of apical segment more than 4 cm long; both margins of pinnae serrate; lamina triangular, the lower pinnae on the larger fronds more than 4 cm long, considerably longer than the upper, acute at the tips; pinnae in lower half of frond with 15–30 sori apiece, the longest more than 5 mm long. . . . . 1. *A. abscissum*.
        11. Serrate portion of apical segment less than 4 cm long; only the anterior and distal pinna margins serrate, the posterior margins mostly entire; lamina lanceolate or narrowly triangular in outline, the lower pinnae less than 4 cm long, only slightly longer than the upper, broadly rounded to obtuse or acutish at the tips; pinnae in lower half of frond with 3–6 sori apiece, the longest less than 5 mm long. . . . . 7. *A. otites*.

#### 1. *Asplenium abscissum* Willd.

Epilithic (at La Selva). *Petiole* 5–23 cm long, dull greenish. *Lamina* 13–26 cm long, 4–16 cm wide, ovate to deltate, once-pinnate. *Pinnae* 6–

11 pairs, (2–)4–9.5 cm long and 8–18 mm broad, sessile, the margins biserrate. Southern Mexico to Bolivia, south Florida, West Indies; widespread in Costa Rica from 50 to 1,800 m.

At La Selva, *A. abscissum* has only been col-

lected from rocks in quebradas toward the back of the property; it appears to be the rarest of our three epilithic *Asplenium* species. Elsewhere, it may be terrestrial.

2. ***Asplenium cirrhatum* Rich. ex Willd.**  
(=*A. radicans* L. var. *cirrhatum* (Rich. ex Willd.) Rosenstock)

Growing on logs, rarely epilithic. *Petiole* 5–13 cm long, glossy and blackish, glabrous. *Lamina* 12.5–23 cm long, 4–10 cm wide, once-pinnate. *Rachis* prolonged apically, sometimes rooting. *Pinnae* 8–17 pairs, 1.5–4 cm long and 0.5–1.2 cm wide, crenate to serrate. Guatemala to Bolivia, West Indies; widespread in Costa Rica from 0 to 2,000 m.

Common in primary forest at La Selva, where it occurs on fallen logs; *A. cirrhatum* and *Polypodium cervina* are the only La Selva ferns that characteristically exploit this habitat. At Finca El Bejuco, near Chilamate, we have seen *A. cirrhatum* growing on rock faces in seepage areas; elsewhere, it may grow on standing trunks.

3. ***Asplenium cuspidatum* Lam.**  
(=*A. auritum* Sw.; *A. pyramidatum* Liebm.)

Epiphyte (at La Selva). *Petiole* (2–)5–30 cm long, dull grayish-green. *Lamina* 5–30 cm long, 2–17 cm wide, lanceolate, simply pinnate to bipinnate or (elsewhere) tripinnate-pinnatifid, terminating in a pinnatifid apex. *Pinnae* subsessile to short-stalked, 6–25 pairs, 1.2–10 cm long and 0.3–3.5 cm wide, entire or serrate to pinnately divided. Southern Mexico to Argentina, south Florida, West Indies; widespread throughout Costa Rica from 0 to 3,300 m.

A common and widespread branch or stump epiphyte in upland and alluvial forest at La Selva, often encountered on downfalls; abundant in cacao. Elsewhere, it may occasionally be epilithic.

The simply pinnate and decomposed forms of *Asplenium cuspidatum* have long been recognized as distinct species however, as pointed out by Stolze (1981), they grade together insensibly and differ consistently in no other respect. In Costa Rica, the variation tends to be altitudinally clinal, with the simply pinnate form (*A. auritum*) more common at lower elevations. The latter form is by far the more common at La Selva. It is easily distinguished from our other *Asplenium* species by its small size, and the usual presence of a basal, acroscopic tooth or hump on each pinna. *Asplenium cuspidatum* s. str. is known from La Selva by a single collection (*Evans & Bowers 3341*, MO), a specimen with bipinnate laminae.

4. ***Asplenium falcinellum* Maxon**

Epiphyte. *Petiole* 8–26 cm long, dull gray-green, glabrous. *Lamina* about 25–42 cm long and 12–22 cm wide, once-pinnate, the terminal segment conform. *Pinnae* 5–14 pairs, lanceolate, 6–16 cm long and 1–2.5 cm wide, stalked, the margins essentially entire. Southern Mexico to Colombia, West Indies; widespread in Costa Rica, from 50 to 1,500 m.

An occasional canopy epiphyte of the primary forest, often growing lower down in trees along creeks.

*Asplenium falcinellum* is extremely similar to, and perhaps conspecific with, *A. juglandifolium* Lam. of South America.

5. ***Asplenium formosum* Willd.**

Epiphytic or epilithic. *Petiole* 0.5–6.5 cm long, glossy and blackish, glabrous, narrowly winged. *Lamina* 6–30 cm long and 1.3–3 cm wide, linear, once-pinnate. *Pinnae* 13–45 pairs, 0.7–1.5 cm long and 2–5 mm wide, sessile, the margins serrate to incised. Southern and western Mexico to Argentina, West Indies; India, Africa; widespread from 0 to 1,800 m in Costa Rica.

Infrequent at La Selva, mostly seen on concrete stairs or walls, wooden bridge abutments and on large tree trunks along the rivers.

6. ***Asplenium holophlebium* Baker**

Epiphyte, the *rhizome* long-creeping. *Petiole* obsolete or ca. 1–8 mm long, green. *Laminae* once-pinnate, somewhat dimorphic. *Sterile lamina* ovate or deltate to obovate, 0.8–2 cm long and 7–12 mm wide, with 1–4 pairs of pinnae. *Fertile lamina* becoming lanceolate, 2–3.5 cm long and 0.8–1.5 cm wide, with 3–15 pairs of pinnae. *Pinnae* alternate, oblong, elliptical or obovate, briefly stalked, apically acute, the margins entire, 5–9 mm long and 1–5 mm wide, each with a single sorus. Costa Rica to Ecuador; known in Costa Rica only from exceptionally wet forests on the Caribbean slope, from the Miravalles massif south to the vicinity of Siquirres, 50 to 1,500 m.

A delicate and diminutive trailing species, quite unlike any other *Asplenium* at La Selva. Climbing on stems and twigs in the understory; occasional in low, damp areas in rich, upland primary forest.

7. ***Asplenium otites* Link**

Epilithic or terrestrial, the *rhizome* erect. *Petiole* 1–8.5 cm long, green. *Lamina* lanceolate, once-pinnate, 5–20 cm long, 1.5–6 cm wide. Free *pinnae* 8–13 pairs, very short-stalked, the larger

ones 0.6–3 cm long and 0.3–1 cm wide, the margins serrate to biserrate. Costa Rica and Panama to South America; from 0 to 2,000 m in Costa Rica.

Known mainly from rocks in quebradas in the southern portion of the property; occasional on steep, muddy banks.

#### 8. *Asplenium pteropus* Kaulf.

Epiphyte. *Petiole* 0.3–6(–9.5) cm long, dull grayish-green. *Lamina* lanceolate, about 3.5–40 cm long, 1–6 cm wide, once-pinnate. *Pinnae* 10–45 pairs, the larger ones 0.6–4 cm long and 2.5–8 mm wide, sessile or very short-stalked, the margins crenate or serrate. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica from 50 to 1,200 m.

Known at La Selva from just two collections, growing as an understory trunk epiphyte (or on the stilt-roots of a palm) in upland primary forest. Our specimens are rather depauperate, falling at the lower end of the scale for most dimensional ranges given above; they would be identified by some authors as *Asplenium pseudoerectum* Hieron., but we follow the treatment of Lellinger (in litt.).

#### 9. *Asplenium repandulum* Kunze

Epilithic (at La Selva), the *rhizome* short-creeping. *Petiole* rather stout, 5.5–25 cm long. *Lamina* 20–30 cm long, 8.5–22 cm wide, once-pinnate. *Pinnae* 8–15 pairs, lanceolate, subsessile, 3–11 cm long, 1–2.5 cm wide, subentire to crenate or serrate. Southern Mexico to Bolivia, West Indies; from 0 to 1,600 m on both slopes in Costa Rica.

Growing on rocks in quebradas; perhaps our commonest *Asplenium* in this habitat.

#### 10. *Asplenium serra* Langsd. & Fischer

Epiphyte, the *rhizome* short-creeping. *Petiole* 7.5–60 cm long, blackish. *Lamina* once-pinnate, 16–80 cm long and (6–)11–30 cm wide. *Pinnae* 7–27 pairs, narrowly lanceolate, stalked, 3.5–20 cm long, (0.4–)1–3 cm wide, sharply serrate marginally, long-acuminate at the apex. *Sori* in a single row on each side of the costa and close to it, strongly oblique to nearly paralleling the costa. Southern Mexico to Argentina, West Indies; Africa; throughout Costa Rica, from 0 to 3,100 m (the specimens from higher elevations tending to be less robust).

A distinctive species, scattered in primary forest at La Selva. *Asplenium serra* may grow either in the canopy, or as an understory trunk epiphyte.

#### 11. *Asplenium serratum* L.

Epiphyte. *Petiole* short, thick, to ca. 5.5 cm long. *Lamina* simple, narrowly oblanceolate, 21–75 cm long, 3.5–16 cm wide, subentire to crenulate or serrate marginally. *Sori* greatly elongated, spreading at a wide angle from the midrib toward the margin. Southern Mexico to Argentina, south Florida, West Indies; from 0 to 1,000 m in Costa Rica, on both slopes.

A trunk or crotch epiphyte (occasionally in the canopy), widely scattered at La Selva, usually in upland primary forest. *Asplenium serratum* is a rosette-forming, “bird’s nest” fern, closely resembling the familiar and often cultivated Old World species *A. nidus* L. and distinctive, at La Selva, in this regard.

#### 5. BLECHNUM L.

Small, somewhat weedy, terrestrial ferns with obsolete *rhizomes* at La Selva (elsewhere sometimes subarborescent, or more often epiphytic and with creeping *rhizomes*). *Fronds* monomorphic (in ours) to dimorphic, the lamina usually (always, at La Selva) deeply pinnatifid to once-pinnate, with free *venation*. *Sori* elongate, borne near the costa, covered by an *indusium* opening toward the costa.

A cosmopolitan genus of 150–220 species, best represented in the Southern Hemisphere. About 50 species are American, ranging from southeastern Alaska to Tierra del Fuego. The 19 or so Costa Rican species occur mostly above 1,000 m. Very closely related to *Salpichlaena*, though hardly to be confused with it.

#### KEY TO THE SPECIES

1. Lateral pinnae fewer than 8 pairs; lamina terminating in a pinna similar to the lateral pinnae; very rare. . . . . 1. *B. gracile*.
1. Lateral pinnae 10 pairs or more, diminishing to a pinnatifid apex.
  2. Basal pinnae not or only slightly reduced, the lamina abruptly narrowed at the base; occasional. . . . . 2. *B. occidentale*
  2. Basal pinnae much reduced, the lamina gradually narrowed at the base; very rare. . . . . 3. *B. polypodioides*

#### 1. *Blechnum gracile* Kaulf.

(=*B. fraxineum* Willd., *B. lellingermanum* L. D. Gómez)

Terrestrial or epilithic, the *rhizome* creeping to suberect. *Petiole* 2.5–33 cm long (usually long-est on fertile fronds), yellowish-brown, scaly. *Lamina* 6–31 cm long and 1.5–15 cm wide, once-pinnate, deltate to narrowly ovate. *Pinnae* 1–6

(–8) pairs, linear to lanceolate, falcate, 1–15 cm long, 0.4–2.5 cm wide (sterile ones widest), the margins subentire. Southern Mexico to Argentina, West Indies; from 50 to 1,300 m in Costa Rica, on both slopes.

*Blechnum gracile* is known by only two collections at La Selva, from a sandbar along the R. Sarapiquí; it is perhaps of ephemeral occurrence in this habitat.

## 2. *Blechnum occidentale* L.

Terrestrial, the *rhizome* creeping or suberect. *Petiole* 4.5–47 cm long, yellowish-brown. *Lamina* 14–45 cm long, 4.5–23 cm wide, once-pinnate, narrowly deltate to lanceolate. *Pinnae* 10–26 pairs, 2.5–13.5 cm long and 0.5–2.1 cm wide, usually somewhat dilated at the base, the margins subentire. Central Mexico to Chile and Argentina, south Florida, West Indies; throughout Costa Rica, from 0 to 3,100 m.

Occasional at La Selva in weedy and secondary growth on alluvial sites, as on the slope above the R. Puerto Viejo near the Estación del Río.

## 3. *Blechnum polypodioides* Raddi (=*B. unilaterale* Sw.)

Terrestrial, the *rhizome* suberect. *Petiole* 2–16.5 cm long, stramineous, sparsely scaly. *Lamina* 12–33 cm long, 1.5–6 cm wide, once-pinnate, narrowly lanceolate. *Pinnae* 20–37 pairs, the basal ones much reduced, the larger ones 0.9–3.1 cm long and 0.2–0.7 cm wide, dilated at the base, the margins entire. Mexico to Paraguay, West Indies; widespread in Costa Rica from 100 to 1,500 m.

This species is known from La Selva by a single collection (Barcock A72, K) from the southern portion of the property. According to the label, it grew on a “clay bank near water in clearings,” where it was “locally uncommon.” It has also been collected in the vicinity of Chilamate.

In addition to the characters given in the key, *Blechnum polypodioides* differs from *B. occidentale* in its generally narrower laminae and shorter, narrower and more numerous pinnae.

## 6. *BOLBITIS* Schott

HENNIPMAN, E. 1977. A monograph of the fern genus *Bolbitis* (Lomariopsidaceae). Leiden Bot. Ser. 2: 1–331.

Terrestrial, epilithic or epiphytic, the *rhizome* brief and erect to short- or long-creeping. *Fronde* dimorphic, the lamina once-pinnate to bipinnatifid. *Venation* reticulate, with or without free

included veinlets. *Sporangia* completely covering the fertile fronds abaxially.

A pantropical genus of 44 species, 14 of which are neotropical. Ten species are known from Costa Rica. Variable though it is, *Bolbitis* can easily be recognized at La Selva by the combination of reticulate venation and compound (though never decomposed), dimorphic fronds.

## KEY TO THE SPECIES

1. Lamina fully pinnate, the terminal pinna resembling the others; pinnae entire to shallowly sinuate; plants epiphytic or epilithic. . . . . 2. *B. nicotianifolia*.
1. Lamina truly pinnate only in the basal part, the upper ½ or more merely deeply pinnatifid; pinnae shallowly crenate to deeply crenately lobed.
  2. Areolae with free included veinlets; common. . . . . 3. *B. portoricensis*.
  2. Areolae lacking free included veinlets; very rare. . . . . 1. *B. aliena*.

### 1. *Bolbitis aliena* (Sw.) Alston

Terrestrial or epilithic, the *rhizome* short-creeping. *Petiole* of sterile lamina 10–50 cm long. *Sterile lamina* 15–45 cm long and 11–30 cm wide, deltate, once-pinnate, the *pinnae* usually 2–4 pairs; basal 1–2 pairs free, the margins subentire to basally lobed. *Fertile lamina* with longer petiole, the pinnae narrower. Southern Mexico to Bolivia, West Indies; in Costa Rica, known only from La Selva, Finca El Bejuco (in nearby Chilamate de Sarapiquí) and the Caribbean slope of the Cordillera de Guanacaste.

*Bolbitis aliena* is known from La Selva by a single collection, from along the Q. Pantano near Line 2800 (the first record of this species from Costa Rica). It is extremely similar in appearance to the much more common *B. portoricensis*, differing in its somewhat smaller size, primary forest habitat and lack of free included veinlets.

### 2. *Bolbitis nicotianifolia* (Sw.) Alston

Epiphytic or epilithic at maturity, the *rhizome* long-creeping in the former instance, short-creeping in the latter. *Petiole of sterile frond* 11–35 cm long, yellowish-brown, variously scaly. *Sterile lamina* 20–70 cm long, (10–)15–40 cm wide, almost always pinnate at maturity (occasionally trifoliolate or even simple in epilithic specimens from other areas); *sterile pinnae* 1–4 pairs, 8–30 cm long, 3.5–8 cm wide, lanceolate, subentire. *Petiole of fertile frond* 24–50 cm long, the lamina usually much shorter, 7.5–24 cm wide. *Fertile pinnae* 4–12 cm long, 1.2–3.5 cm wide. Guatemala to Peru and the Guianas, West In-

dies; from 0 to 1,500 m in Costa Rica, on both slopes.

An extremely variable, yet distinctive species, *Bolbitis nicotianifolia* is unique among La Selva ferns in exploiting two distinct habitats, in each of which it displays a distinctly different growth form. Atop rocks in fast-moving quebradas, where they are perhaps most abundant, the plants are briefly rhizomatous, suberect, and frequently with a reduced number of pinnae. *B. nicotianifolia* is also widespread in the primary forest, however, where (in sharp contrast to the above habitat) it prefers dimly lit understory situations. Here, the young plants are terrestrial, widely creeping and with simple leaves; ultimately, however, a suitable treelet is encountered and ascended to a height of 2 m or more. Mature forest individuals have long, appressed rhizomes (which may lose the connection with the ground) and spreading, fully-pinnate fronds.

3. ***Bolbitis portoricensis*** (Sprengel) Hennisman  
(=*B. cladorrhizans* (Sprengel) Ching)

Terrestrial, or rarely epilithic, the *rhizome* short-creeping. *Petiole of sterile frond* 14–60 cm long, yellowish-brown. *Sterile lamina* 21–63 cm long, 16–45 cm wide, pinnate, deltate, sometimes apically proliferous. *Sterile pinnae* 4–11 pairs, the basal 3–6 free, mostly 12–34 cm long, 1.8–8.5(–15) cm wide, the margins subentire to crenately lobed; basal pinnae deeply pinnatifid. *Petiole of fertile lamina* 11–60 cm long. *Fertile lamina* 10–50 cm long, 3.5–38 cm wide, with up to 12 pairs of pinnae, these much narrowed, 2–16 cm long and 0.4–5.5 cm wide. Southern Mexico to Ecuador and Venezuela, West Indies; widespread in Costa Rica, from 0 to 1,000 m.

Of scattered occurrence at La Selva, mostly on alluvial sites in cacao groves and old secondary forest; rare on rocks in forest streams (Q. Esquina).

7. **CTENITIS** (C. Chr.) C. Chr.

CHRISTENSEN, C. 1920. A monograph of the genus *Dryopteris*, part II. The tropical American bipinnate-decompound species. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. Ser. 8, 6: 3–132.

SMITH, A. R. AND R. C. MORAN. 1987. New combinations in *Megalastrum* (Dryopteridaceae). Amer. Fern J. 77: 124–130.

Terrestrial plants, usually in second growth at La Selva. *Rhizome* obsolete, the *lamina* relatively large, monomorphic, tripinnatifid to tripinnate, with free *venation*. *Sori* round, abaxial. *Indusium* present or (in ours) lacking.

*Ctenitis* includes 110–130 species and is pan-tropical, with about 70 species in the New World ranging from central Mexico, South Florida and Bermuda to Chile. About 24 species are known from Costa Rica.

Both La Selva species have the aspect of juvenile tree-ferns, but those Cyatheaceae with decompound laminae have spinose petioles, and are never fertile while still acaulescent. Other, smaller ferns that might be confused are *Tectaria mexicana* (with reticulate venation), *Lastreopsis exculta* (a much smaller plant) and, especially, *Thelypteris torresiana* (with the stipe basally glaucous). Our *Ctenitis* species are both relatively rare.

KEY TO THE SPECIES

1. Scales of stipe, rachis, costae and costules pale to reddish-brown; basal posterior pinnule of basal pinnae more than 10 cm long, about ½ as long as the pinna itself; lamina drying bright green. . . . . 1. *C. sloanei*.
1. Scales of stipe, rachis, etc. dark brown; basal posterior pinnule of basal pinnae less than 10 cm long, about ½ as long as the pinna itself; lamina drying grayish-green. . . . . 2. *C. subincisa*.

1. ***Ctenitis sloanei*** (Poeppig ex Sprengel) C. Morton

*Petiole* 24–70 cm long, densely clothed at the base with woolly, reddish scales. *Lamina* 38–71 cm long, deltate, 4-pinnate at base, bipinnate-pinnatifid in upper part. *Pinnae* about 12–15 pairs, the lowermost 20–50 cm long and 14–23 cm wide. Southern Mexico to Ecuador and Venezuela, south Florida, West Indies; widespread from 0 to 1,800 m in Costa Rica.

Very rare at La Selva, with only a few plants seen in more or less disturbed, alluvial forest.

2. ***Ctenitis subincisa*** (Willd.) Ching  
(=*Megalastrum subincisum* (Willd.) A. R. Smith & R. C. Moran)

*Petiole* to 60 cm long or more, densely clothed at base with dark brown scales. *Lamina* 60–100 cm or more long, deltate, tripinnate-pinnatifid below. *Pinnae* 14–17 pairs, the largest (basal) ones 26–50 cm or more long, 9–25 cm or more wide. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica from 0 to 2,100 m.

Growing in somewhat disturbed, alluvial sites where it may be locally abundant, as along the Lindero Occidental at about Line 900. *Ctenitis subincisa* is rather uncommon at La Selva, though more frequent than *C. sloanei*.

This species would fall into the recently seg-

regated genus *Megalastrum* Holttum (see Smith & Moran, 1987), which differs from *Ctenitis* s. str. in lacking clathrate scales on the frond axes and unicellular glands on the young indusia.

#### 8. CYCLOPELTIS J. Smith

Terrestrial ferns, the *rhizome* erect. *Lamina* monomorphic, lanceolate, once-pinnate, the pinnae numerous. *Venation* free. *Sori* abaxial, round, with peltate indusia.

A genus of 3–6 species of tropical Asia and the Americas. The single neotropical species ranges from Chiapas to Bolivia, and throughout the West Indies. It most resembles species of *Nephrolepis*, but differs in having two rows of sori between the costa and pinna margin.

##### 1. *Cyclopeltis semicordata* (Sw.) J. Smith

*Petiole* 5–37 cm long. *Lamina* lanceolate, 0.4–1.6 m long, 12–30 cm wide, once-pinnate. *Pinnae* alternate, linear-lanceolate, 4.5–16 cm long, 1–2 cm wide, sessile, semicordate and auriculate basally, the margins subentire. Occurring on both coasts of Costa Rica from 0 to 1,000 m, but most common below 400 m.

*Cyclopeltis semicordata* is common at La Selva in secondary growth and along streams in alluvial sites.

#### 9. DENNSTAEDTIA T. Moore

TRYON, R. 1960. A review of the genus *Dennstaedtia* in America. *Contr. Gray Herb.* 187: 23–52.

Generally coarse, terrestrial ferns, the *rhizome* short- to long-creeping. *Lamina* monomorphic, bipinnate-pinnatifid to 4-pinnate (in ours). *Venation* free. *Sori* marginal, the indusium pouch-like.

A genus of 45–50 species, essentially pantropical, but with some temperate species in both hemispheres. The 12 New World species range from eastern Canada to central Chile, and throughout the West Indies. Nine of these occur in Costa Rica.

The only taxa at La Selva with which *Dennstaedtia* can be confused are *Hypolepis* (which differs in having spiny petioles and rachises) and *Saccoloma inaequale* (a smaller fern with an erect rhizome and different soral structure).

#### KEY TO THE SPECIES

1. *Lamina* tripinnate-pinnatifid to partly 4-pinnate; rachis and costae glabrous, or with a sparse to moderately dense indumentum of spreading, whitish hairs; rhizome and very base of petiole covered with

multicellular trichomes; plants of secondary forest and disturbed sites on alluvium.

2. Rachis, costae, costules and major veins glabrous, or with occasional and remote trichomes; tufts of brownish trichomes present in the axils of the pinnae, pinnules and ultimate segments; trichomes of rhizome and petiole base somewhat spreading, short, reddish-brown; locally abundant in secondary growth and disturbed areas in alluvial forest. . . . . 1. *D. bipinnata*.
2. Rachis, costae, costules and major veins (above and below) sparsely to densely pubescent with whitish, spreading trichomes; axils lacking tufts of brownish trichomes; trichomes of rhizome and petiole base closely appressed and matted, longish, tawny; very rare plants of open sites along major rivers. . . . . 2. *D. cicutaria*.
1. *Lamina* bipinnate-pinnatifid to partly 3-pinnate; costae, costules and rachis (at least apically) covered below with a close, brownish, scurfy indumentum of curled trichomes; axils of segments lacking tufts of trichomes; rhizome and base of petiole glabrous; plants of the primary forest. . . . . 3. *D. obtusifolia*.

##### 1. *Dennstaedtia bipinnata* (Cav.) Maxon

*Rhizome* long-creeping, subterranean. *Fronde*s distant, 2–3 m long. *Petiole* to at least 50 cm long, glossy, bicolored (dark brown above, green below). *Lamina* to at least 75 cm long, tripinnate-pinnatifid to 4-pinnate, the *basal pinnae* 25–70 cm long and 10–30 cm wide. Southern Mexico to Bolivia, West Indies; from 0 to 1,800 m on both slopes of Costa Rica.

This is the most common *Dennstaedtia* at La Selva, growing in weedy areas and secondary growth on alluvial sites. It may be locally abundant, as in low-lying parts of the Arboretum.

##### 2. *Dennstaedtia cicutaria* (Sw.) T. Moore

*Rhizome* short-creeping. *Fronde*s 1.5–3.5 m long. *Petiole* 0.5–1.5 m long, dull brown, darker toward base. *Lamina* 0.75–2 m long, 0.75–1 m wide, deltate, tripinnate to 4-pinnatifid. *Basal pinnae* 40–60 cm or more long, 17–35 cm wide. Southern Mexico to Argentina, West Indies; widespread in Costa Rica from 50 to 1,300 m.

Locally abundant at La Selva in riparian growth along the R. Sarapiquí, at the base of Avenida Marañón.

##### 3. *Dennstaedtia obtusifolia* (Willd.) T. Moore

*Rhizome* short-creeping, often exposed. *Fronde*s to 3 m long. *Petiole* 50–100 cm long, dull brown. *Lamina* to at least 1.25 m long and 1 m wide, bipinnate-pinnatifid to partly tripinnate. *Basal pinnae* 35–72 cm long, 14–30 cm wide. Southern Mexico to Paraguay, West Indies; widespread from 0 to 2,100 m in Costa Rica.



*Dennstaedtia obtusifolia* appears restricted to primary forest at La Selva, where it is uncommon and generally found along small streams, such as the Q. Arboleda near the Sendero Hartshorn.

*Dennstaedtia obtusifolia* is closely related to and perhaps conspecific with *D. dissecta* (Sw.) T. Moore.

#### 10. DICRANOGLOSSUM J. Smith

CHRISTENSEN, C. 1929. Taxonomic fern-studies. I. Revision of the polypodioid genera with longitudinal coenosori (Cochlidiinae and "Didymoglossinae"); with a discussion of their phylogeny. Dansk Bot. Ark. 6(3): 1-93.

Epiphytic ferns, the *rhizome* short. *Lamina* subdichotomously divided into lanceolate segments bearing elongate, marginal *sori*.

A neotropical genus of 3-6 species ranging from Guatemala and Cuba south throughout the northern half of South America. A single species occurs in Costa Rica.

*Dicranoglossum* is instantly recognized by the manner of frond dissection. *Hecistopteris pumila* also has dichotomously divided fronds, but the *sori* are abaxial and the plants are an order of magnitude smaller.

##### 1. *Dicranoglossum panamense* (C. Chr.) L. D. Gómez

*Petiole* winged, brief. *Lamina* 14-39 cm long, with 3-9 *segments*, these 3-12 mm wide, long-acuminate apically, the margins entire. Honduras to Colombia; from 0 to 700 m in Costa Rica, on both coasts.

Occasional at La Selva, mostly as a low branch epiphyte in old secondary forest and cacao on alluvial sites.

Tryon and Tryon (1982) regarded *Dicranoglossum panamense* as conspecific with *D. polypodioides* (Hook.) Lellinger of Ecuador, however the latter differs strikingly in its discrete, round *sori*, and most other authorities continue to recognize both entities.

#### 11. DIDYMOCHLAENA Desv.

Terrestrial fern, the *rhizome* erect. *Laminae* monomorphic, bipinnate, the *ultimate segments*

(pinnules) dimidiate. *Venation* free. *Sori* abaxial, elliptic, indusiate.

A monotypic, pantropical genus, ranging in the New World from southern Mexico and Cuba to Uruguay.

The dimidiate pinnule morphology in this genus is reminiscent of *Adiantum* and *Lindsaea*, from both of which *Didymochlaena* may be distinguished by its elliptical *sori* borne along the veins, perpendicular to the margin.

##### 1. *Didymochlaena truncatula* (Sw.) J. Smith

*Petiole* 25-63 cm long, densely scaly at the base. *Lamina* 54-110 cm long, ovate to broadly lanceolate, bipinnate, with 14-20 pairs of *pinnae*, these 14-30 cm long. *Pinnules* oblong, 0.9-2.5 cm long, 0.5-1.2 cm wide, subentire to crenulate marginally. Widespread in Costa Rica from 0 to 1,500 m.

A striking fern, scattered at La Selva in low, wet areas in primary or somewhat disturbed forest on alluvial sites.

#### 12. DIPLAZIUM Sw.

Virtually always terrestrial in Costa Rica, the *rhizome* more or less erect. *Lamina* monomorphic (in ours) or somewhat dimorphic, simple (elsewhere) to pinnatifid, or once-pinnate to tripinnate. *Venation* most often free, occasionally reticulate. *Sori* linear, abaxial, indusiate, at least some (usually on the basal *pinnae*) borne in back-to-back pairs.

The occasionally paired *sori* and consistently terrestrial habit at La Selva combine to distinguish *Diplazium* from the often very similar *Asplenium*. Compare also with *Hemidictyum*. *Diplazium lechleri* (Mett.) T. Moore, which occurs at somewhat higher elevations in the Sarapiquí region, is facultatively epiphytic.

A worldwide, largely tropical genus of 300-400 species, the 100 or so New World species ranging from eastern Canada south to Uruguay, and throughout the West Indies. There are about 50 Costa Rican species.

#### KEY TO THE SPECIES

1. *Lamina* deeply tripinnatifid to essentially tripinnate; very rare in swamp forest. . . . . 3. *D. ingens*.
1. *Lamina* pinnate to bipinnatifid.
  2. Veins anastomosing, the venation reticulate; margins of petiole scales black, with stout, black, bifurcate processes; only the *pinnae* in the basal part of the *lamina* truly free, the upper 1/2 or more merely pinnatifid. . . . . 7. *D. pactile*.
  2. Venation free; petiole scales lacking marginal forked processes; apical pinnatifid portion much less than 1/2 the length of the *lamina*.

3. Pinnae subentire to crenate or serrate, never lobed to  $\frac{1}{2}$  the distance to the midvein; very rare. . . . . 2. *D. grandifolium*.
3. Pinnae, at least the basal ones, regularly lobed, to halfway to the midvein or further.
  4. Lamina narrowly lanceolate, less than 15 cm wide; pinnae less than 2 cm wide, acute or (more frequently) with long-attenuate serrate tips  $\frac{1}{4}$  to  $\frac{1}{3}$  as long as the pinna itself; sori generally in one row on each side of the costa (i.e., one per lobe). . . . . 5. *D. lonchophyllum*.
  4. Lamina deltate to broadly lanceolate, more than 15 cm wide; pinnae (at least the basal ones) more than 2 cm wide, with acute to long-attenuate serrate tips, but much less than  $\frac{1}{4}$  as long as the pinna; sori several to many per pinna lobe, at least on the basal pinnae.
    5. Pinnae, at least in the basal half of the frond, lobed to at least  $\frac{1}{5}$  the way to the costa, each lobe with more than 9 pairs of sori.
      6. Fronds very large, the pinnae (at least the basal ones) more than 8 cm wide; lamina often producing buds; lobes of the pinnae acute to acuminate, entire or obscurely toothed, the margins plane. . . . . 6. *D. macrophyllum*.
      6. Fronds smaller, the pinnae always less than 8 cm wide; lamina not producing buds; lobes of pinnae rounded to acute, denticulate to lobed, the margins revolute. . . . . 4. *D. lindbergii*.
    5. Pinnae lobed much less than  $\frac{1}{5}$  the way to the costa (an occasional lobe may be very deep), each with less than 9 pairs of sori.
      7. Rachis and costae minutely pubescent below; free pinnae more than 20 pairs; plants often with a trunk, to 1.5 m tall; common. . . . . 8. *D. striatastrum*.
      7. Rachis and costae essentially glabrous; free pinnae less than 20 pairs; plants never subarborescent; very rare. . . . . 1. *D. cristatum*.

### 1. *Diplazium cristatum* (Desr.) Alston

*Petiole* 16–51 cm long. *Lamina* more or less ovate, 23–50 cm long, once-pinnate. *Pinnae* lanceolate, 5–17 cm long, 1.5–4 cm wide, crenately lobed to deeply pinnatifid, the basal ones often with one free basal, anterior lobe. Southern Mexico to Argentina, West Indies; from 0 to 2,000 m in Costa Rica.

Very rare at La Selva, known only from low, wet, relatively intact alluvial forest (Discovery Woods, etc.). *Grayum* 2066, from along the lower part of the Q. El Salto, differs from this species in its longer (more than 80 cm) fronds and longer (to more than 7 mm), more oblique sori, and in having the stalks of the pinnae undulate-winged and the rachis, costae and costules elevated and prominently channeled and winged. It may represent a hybrid, or perhaps an additional species.

### 2. *Diplazium grandifolium* (Sw.) Sw.

*Petiole* 14–62 cm long. *Lamina* 39–79 cm long, once-pinnate. *Pinnae* 8–13 pairs, the lower ones short-stalked; larger pinnae 8–19 cm long, 2–4 cm wide, truncate to broadly cuneate basally, entire to crenulate marginally. Guatemala to Peru and Venezuela, West Indies; widespread in Costa Rica from 0 to 2,000 m.

Known from La Selva by a single collection, from the lower part of the Q. El Salto.

### 3. *Diplazium ingens* Christ

*Fronds* to 3 m long or more. *Lamina* tripinnatifid, ovate, ca. 1.2 m wide, the largest *pinnae* to 60 cm long and 25 cm wide. *Pinnules* 9–13

cm long, pinnatifid nearly to the costule, the *ultimate segments* crenate to serrate. Known only from northeastern Costa Rica to central Panama (Cocles); in Costa Rica, restricted to below 200 m on the Caribbean coast.

Our only *Diplazium* with decompose blades, *D. ingens* is known from La Selva by a single collection from near an open, marshy area at the southwest corner of the Western Annex.

### 4. *Diplazium lindbergii* (Mett.) Christ

*Fronds* to 1.5 m long. *Petiole* to 80 cm long, generally longer than the lamina. *Lamina* ovate, pinnate-pinnatifid. *Pinnae* 12–20 pairs, the larger ones 18–30 cm long, 3.5–7.5 cm wide, deeply pinnatifid. *Lobes* rounded to obtuse or acute apically, the margins more or less revolute and serrulate. Southern Mexico to Bolivia; widespread in Costa Rica from 0 to 2,100 m.

Fairly common at La Selva in low, wet areas, especially in primary swamp forest.

### 5. *Diplazium lonchophyllum* Kunze

*Rhizome* to about 10 cm long, erect or reclining. *Petiole* about 9–25 cm long. *Lamina* lanceolate, about 20–40 cm long, once-pinnate. Free *pinnae* 11–17 pairs, the larger ones 4.5–8 cm long and 1–1.5 cm wide, narrowly lanceolate, acute to long-acuminate apically, the basal ones deeply lobed. Southern Mexico to Panama; from 0 to 2,000 m in Costa Rica.

Rare at La Selva, growing along rivers and lower portions of major quebradas, frequently among rocks as at the waterfall on the Q. El Salto.

The habitat and the aspect are those of a rheophyte.

6. **Diplazium macrophyllum** Desv.  
(=*D. ceratolepidioides* Losch)

*Fronde*s to at least 2 m long, the petiole and lamina subequal (or the petiole somewhat shorter). *Lamina* ovate-lanceolate, pinnate-pinnatifid, the largest pinnae about 30–50 cm long and 13–20 cm wide, long-stalked. *Lobes* of pinnae acute to acuminate, the margins entire to obscurely toothed; often viviparous. Costa Rica to Ecuador; widespread in Costa Rica from 0 to 1,600 m.

Locally common at La Selva in swampy areas and along sluggish sections of creeks.

7. **Diplazium pactile** Lellinger

*Petiole* 25–80 cm long, the scales black-margined and with stout, black, bifurcate marginal processes. *Lamina* subequal to longer than petiole, once-pinnate. *Pinnae* 5–8 pairs, lanceolate, about 14–25 cm long and 4–8 cm wide, subentire to sinuate marginally, the basal ones sessile or free and short-stalked. Costa Rica to Ecuador; from 50 to 500 m on the Caribbean slope of Costa Rica.

Occasional at La Selva in primary swamp forest, and along sluggish sections of quebradas.

*D. pactile* is distinctive among our species of *Diplazium* in its peculiar petiolar scales and sparingly divided blades with anastomosing sori.

8. **Diplazium striatastrum** Lellinger

*Rhizome* erect, forming a small trunk to at least 1.5 m tall. *Petiole* 20–55 cm long. *Lamina* lanceolate, 30–100 cm long, pinnate-pinnatifid. *Pinnae* numerous, the largest 9.5–20 cm long and 2–3 cm wide, subsessile to short-stalked, crenately lobed about halfway to the costa. Southern Mexico to Ecuador and Venezuela; widespread in Costa Rica from 0 to 1,600 m.

Quite common at La Selva in secondary growth and old cacao on alluvial sites, as between the Estación del Río and the pejibaye grove.

*Diplazium striatastrum* is our only non-cyatheaceous fern that develops an erect trunk of any consequence. It is closely related to *D. striatum* (L.) C. Presl, with which it has been included by many authors.

N.B.: *Diplazium ceratolepis* (Christ) L. D. Gómez is represented from La Selva by *Scamman* 7471 (CR), a fragmentary, though unquestionably correctly identified, specimen. This species is closely related to *D. pactile*, with which

it shares reticulate venation and the peculiar, blackmargined petiolar scales bearing forked, hornlike marginal processes; it is, however, more superficially similar to *D. macrophyllum* in its relatively large fronds and uniformly deeply incised pinnae. We suspect the Scamman collection to have been mislabeled, since it seems highly unlikely that all collectors who worked at La Selva during the more than 30 years that have elapsed since Scamman's comparatively brief visits would have overlooked such a striking fern; furthermore, we have seen no other Costa Rican collection of *Diplazium ceratolepis* from below 300 m. Nonetheless, future workers should keep a sharp eye out for this species in the swamp or streamside habitats that (along with *D. pactile* and *D. macrophyllum*) it favors.

13. **ELAPHOGLOSSUM** Schott ex J. Smith

CHRIST, H. 1899. Monographie des Genus *Elaphoglossum*. Denkschr. Schweiz. Naturf. Ges. 36: 1–159.

GÓMEZ P., L. D. 1975. Contribuciones a la pteridología costarricense. VI. El género *Peltapteris* Link en Costa Rica. Brenesia 6: 25–31.

MICKEL, J. T. 1981. *Elaphoglossum* Schott ex J. Sm. Pp. 210–238 in R. G. STOLZE, Ferns and fern allies of Guatemala. Part II. Fieldiana, Bot. n.s. 6: 1–522.

Epiphytic at La Selva (though often terrestrial elsewhere, especially at higher elevations). *Rhizome* suberect to long-creeping. *Fronde*s dimorphic, the *sterile lamina* simple and entire to subdichotomously divided into linear lobes. *Venation* generally free. *Fertile lamina* always simple and subentire, completely covered with sporangia abaxially.

*Elaphoglossum* is easily recognized by its dimorphic fronds, with at least the fertile ones simple and entire. *E. peltatum* differs strikingly from the rest of our species in its finely dissected sterile laminae, and has often been assigned to a segregate genus, *Peltapteris* Link.

A pantropical and south temperate genus of 500–600 species, about 350 of which are American. The latter range from northern Mexico and Cuba south to southern Chile. *Elaphoglossum* is one of the largest pteridophyte genera in Costa Rica, with perhaps 100 species, most of which occur above 1,000 m; about a fourth of these are still undescribed (J. T. Mickel, pers. comm.). *E. backhousianum* T. Moore has been collected from the Sarapiquí lowlands, near Chilamate.

KEY TO THE SPECIES

1. Sterile lamina several times dichotomously divided into linear lobes; fertile lamina suborbicular; rhi-

- zome slender, long-creeping, the fronds distant. . . . . 5. *E. peltatum*.
1. Sterile lamina simple, entire; fertile lamina ovate to lanceolate; rhizome various.
  2. Rhizome long-creeping, the fronds distantly spaced. . . . . 1. *E. amygdalifolium*.
  2. Rhizome very short, the fronds closely approximate.
  3. Sterile lamina thick, waxy, brittle, pendulous, to more than 50 cm long, the lateral veins obscure; reddish rhizome scales very dense, conspicuous, usually more than 2 cm long; fertile lamina more than 3 cm wide, cordate to rounded or truncate basally; canopy epiphyte. . . . . 2. *E. herminieri*.
  3. Sterile lamina more or less normally leafy in texture, less than 50 cm long, the lateral veins distinguishable; scales of rhizome less than 2 cm long; fertile lamina less than 3 cm wide, attenuate basally.
  4. Largest sterile laminae more than 5 cm wide; lamina often dark, gun-metal green; canopy epiphyte. . . . . 3. *E. latifolium*.
  4. Largest sterile laminae less than 5 cm wide; lamina bright green; plants often growing in the understory.
  5. Sterile lamina more than 23 cm long, acutish to acuminate apically, usually with some scattered stellate trichomes on the lower surface; glands lacking; small reddish scales apparent on the rhizome about the stipe bases. . . . . 6. *E. sp. nov. ined.*
  5. Sterile lamina less than 23 cm long, broadly rounded to acutish at the apex, usually glabrous except on the margins; microscopic yellowish glands present on leaf surfaces and midribs, most obvious toward the bases of the stipes; rhizome scales few and distant, rarely noticeable. . . . 4. *E. palmense*.
1. ***Elaphoglossum amygdalifolium*** (Mett. ex Kuhn) Christ  
*Rhizome* long-creeping. *Sterile lamina* 9–21 cm long and 1.5–2 cm wide, simple and entire, linear-lanceolate, thin, acuminate at apex, the *petiole* 0.1–2.2 cm long. *Fertile lamina* narrower, to ca. 15 cm long, 5–12 mm wide, the *petiole* 1–5 cm long. Guatemala to Colombia, Cuba; from 50 to 1,500 m in Costa Rica, chiefly on the Caribbean slope.  
Occasional, usually seen creeping on twigs or stems of shrubs in the understory of relatively intact alluvial forest, often along creeks. The new leaves are pinkish.
  2. ***Elaphoglossum herminieri*** (Bory ex Fée) T. Moore  
*Rhizome* short-creeping, the scales orange, dense, 15–30 mm long. *Petiole* obsolete. *Sterile lamina* linear-lanceolate, simple, long-attenuate at base, to 1(–2) m long and 3.5–5.5 cm wide, thick, bluish-green, waxy and brittle, pendent. *Fertile lamina* 7–15 cm long and 3–5.5 cm wide, cordate to truncate basally. Guatemala to Venezuela, West Indies; from 0 to 500 m on the Caribbean coast of Costa Rica.  
A canopy epiphyte, widespread in primary forest; conspicuous, though seldom seen in fertile condition. The thick, narrow, pendent sterile fronds give this plant the superficial aspect of an *Anthurium* sp. (Araceae).
  3. ***Elaphoglossum latifolium*** (Sw.) J. Smith  
(=*E. cismense* Rosenstock; *E. tovariense* (Moritz ex D. Eaton) T. Moore)  
*Rhizome* short-creeping. *Sterile lamina* 24–50(–70) cm long and 3.5–7 cm wide, lanceolate, coriaceous, dark (often bluish-) green, the *petiole* 2–18 cm long. *Fertile lamina* generally narrower, longer-stalked. Southern Mexico to Bolivia, West Indies; widespread from 50 to 2,100 m in Costa Rica.  
A canopy epiphyte, scattered throughout in upland primary forest; most often seen on downfalls.
  4. ***Elaphoglossum palmense*** Christ  
(=*E. firmulum* Rosenstock)  
*Rhizome* suberect. *Sterile lamina* linear to narrowly oblanceolate or spatulate, 8–22 cm long and 1.2–2.6 cm wide, the *petiole* obsolete to 1.1 cm long. *Fertile lamina* 3.5–8.5 cm long and 4–7 mm wide, the *petiole* 5–13.5 cm long. Nicaragua to Colombia (Chocó); from 0 to 2,000 m in Costa Rica, chiefly on the Caribbean slope of the Cordillera Central.  
Scattered at La Selva in upland primary forest; occasional in the understory, but principally a canopy epiphyte, most frequently encountered on downfalls.  
Costa Rican material of this species has often been misidentified as *Elaphoglossum nigrescens* (Hook.) T. Moore ex Diels.
  5. ***Elaphoglossum peltatum*** (Sw.) Urban  
(=*Peltapteris peltata* (Sw.) C. Morton; *E. flabellatum* (Humb. & Bonpl.) Christ; *E. foeniculaceum* (Hook. & Grev.) C. Chr.)  
*Rhizome* slender, long-creeping. *Petioles* sparsely but obviously scaly, those of the sterile fronds 1–7(–9.5) cm long. *Sterile lamina* 1–3(–6) cm long and about equally as broad, fan-shaped to more or less circular, deeply dichotomously dissected. *Ultimate segments* 0.5–1.5

mm wide. *Petiole of fertile fronds* 1.5–10.5 cm long, the *lamina* roughly orbicular, 5–16 mm across. Southern Mexico to Venezuela and Peru, West Indies; widespread in Costa Rica from 0 to 3,000 m.

A delicate, diminutive fern, our only *Elaphoglossum* with divided blades. Common throughout in primary forest; mainly a canopy branch epiphyte, very frequent on downfalls.

6. *Elaphoglossum* sp. nov. ined.

*Rhizome* short-creeping. *Sterile fronds* 22–30 cm long, the *petioles* to about 5 cm long. *Sterile lamina* 2.9–3.6 cm wide, narrowly oblanceolate, the apex acuminate. *Fertile fronds* narrower, with a much longer petiole. The overall distribution of this as yet undescribed species is not known to us, but it is probably confined, in Costa Rica, to the Caribbean lowlands.

An understory epiphyte, the plants often densely clothing the trunks of medium-sized trees to a height of 2–6 m in low, rich primary forest. This species is soon to be described by Dr. John T. Mickel (pers. comm.).

14. GRAMMITIS Sw.

BISHOP, L. E. 1978. Revision of the genus *Cochlidium* (Grammitidaceae). Amer. Fern J. 68: 76–94.

COPELAND, E. B. 1952. The American species of *Xiphopteris*. Amer. Fern J. 42: 41–52, 93–110.

Usually small, epiphytic or epilithic ferns. *Rhizome* generally obsolete to brief, the *laminae* essentially monomorphic, simple and entire to serrate or variously lobed, or deeply pinnatifid to once-pinnate or, more rarely, more extensively compound. *Venation* almost always free. *Sori* round, discrete or (as in ours) confluent into a coenosorus, abaxial, exindusiate.

*Grammitis* is closely related to *Polypodium*, from which it may usually be distinguished by having non-articulate petioles, spreading, unicellular, often brownish trichomes on the petioles and laminae (ours essentially glabrous) and pale green, chlorophyllous spores, and in lacking petiolar scales. The two La Selva species of *Grammitis* are distinctive and somewhat atypical in having simple, linear laminae and sporangia borne in apparent (*G. serrulata*) or true (*G. linearifolia*) coenosori, and are not likely to be confused with any of our species of *Polypodium*. Although *G. linearifolia* has usually been referred to the satellite genus *Cochlidium*, which has occasionally been expanded (Bishop, 1978) to accommodate *G. serrulata* as well, we follow Tryon and Tryon (1982) and Proctor (1985) in including both within the large and exceedingly variable *Grammitis*.

*Grammitis*, in the broad sense adopted here, is a pantropical and south temperate genus of about 400 species. The 175 or so New World members range from central Mexico and Cuba south to Tierra del Fuego. About 72 species occur in Costa Rica, the vast majority above 1,000 m.

KEY TO THE SPECIES

1. Lamina entire. . . . . 1. *G. linearifolia*.  
1. Lamina deeply serrate. . . . . 2. *G. serrulata*.

1. **Grammitis linearifolia** (Desv.) Steudel  
(=*Cochlidium linearifolium* (Desv.) Maxon  
ex C. Chr.)

Epiphyte. *Rhizome* stout, erect, the leaves tufted. *Petiole* very short or obsolete. *Lamina* simple, entire, narrowly linear, 3–10(–20) cm long, 1–3 mm wide, usually somewhat curved. Guatemala and Belize to Brazil; generally a lowland species from below 350 m, but ranging occasionally to at least 2,200 m in Costa Rica.

Common at La Selva in primary forest, mainly as a canopy branch epiphyte, and frequently encountered on downfalls. This is one of the few epiphytic ferns frequently encountered on the otherwise barren upper limbs of *Pentaclethra maculosa* (Willd.) Kuntze. Though relatively distinctive, it may be confused with precociously fertile juveniles of *Vittaria lineata*.

2. **Grammitis serrulata** (Sw.) Sw.  
(=*Cochlidium serrulatum* (Sw.) L. Bishop;  
*Xiphopteris serrulata* (Sw.) Kaulf.)

*Rhizome* elongate, filiform, ascending. *Petiole* obsolete or to about 2 cm long. *Lamina* linear, 2–8 cm long, 0.5–3.5 mm wide, marginally serrate. Southern Mexico to Bolivia, West Indies; Africa; widespread in Costa Rica from 0 to 2,000 m.

A diminutive yet distinctive fern, very frequent at La Selva. It is characteristically a canopy branch epiphyte, but is most commonly encountered on downfalls.

N.B.: *Scamman 7519* (CR), attributed to La Selva, is a correctly identified specimen of *Grammitis turrialbae* (Christ) F. Seymour. Since this species is not otherwise known from below about 1,800 m elevation in Costa Rica and no other La Selva specimens have been seen, a label mix-up seems virtually certain. *G. turrialbae* is easily distinguished from the two *Grammitis* species treated above by its larger (10–40 cm long), fully pinnate laminae (with 25–70 pairs of pinnae, the largest 1.4–6.8 cm long). It rather resembles a *Polypodium*, and would more or less key out to

that genus in the present treatment, but differs from all of our species of *Polypodium* in its spreading, brownish petiolar trichomes.

#### 15. HECISTOPTERIS J. Smith

Diminutive, short-creeping epiphytes with simple, monomorphic *laminae* that are apically forked, or subdichotomously divided into short, broad, apiculate lobes. *Venation* free. *Sori* somewhat elongate (sometimes fused) and abaxial, ex-indusiate.

A monotypic, neotropical genus ranging from southern Mexico and Cuba to southwestern Brazil.

##### 1. *Hecistopteris pumila* (Sprengel) J. Smith

*Rhizome* filiform, creeping. *Lamina* subsessile, wedge- or fan-shaped, 0.75–2(–3) cm long, 1–6 mm wide, apically notched or several times subdichotomously cleft into acute lobes, the margins entire. From 0 to 1,000 m in Caribbean and southwestern Costa Rica.

At La Selva, *Hecistopteris pumila* appears to be principally a canopy branch epiphyte, and is most likely to be encountered on downfalls. Although it must be easily overlooked, *H. pumila* appears to be truly uncommon or even rare at La Selva. This and *Trichomanes angustifrons* are our smallest ferns.

#### 16. HEMIDICTYUM C. Presl

Coarse, terrestrial ferns with a stout, erect *rhizome*. *Fronde* large, monomorphic, once-pinnate. *Venation* reticulate. *Sori* linear, indusiate, abaxial.

Although the general description recalls that of *Diplazium*, in which *Hemidictyum* has sometimes been included, this is a very striking, distinctive and easily recognized fern. The large, thin, entire, opposite pinnae are somewhat auriculate at the base, and oriented obliquely with respect to the rachis, giving the plant a somewhat zingiberoid aspect.

A monotypic, neotropical genus ranging from southern Mexico and Cuba to southeastern Brazil.

##### 1. *Hemidictyum marginatum* (L.) C. Presl (=*Diplazium marginatum* (L.) Diels)

*Petiole* stout, to about 1 m long. *Lamina* 1–2 m long, oblong, once-pinnate, the terminal pinna similar to the rest. *Pinnae* 5–10 pairs, 25–55 cm long, 6–12 cm wide, cordate-clasping basally, the margins entire. Widespread in Costa Rica from 0 to 1,600 m.

At La Selva, *H. marginatum* is known only from riparian habitats along the rivers and lower portions of major quebradas. It is a rare fern here, seldom observed in spite of its size and unusual aspect and the fact that it occurs near heavily frequented areas.

#### 17. HEMIONITIS L.

Essentially terrestrial ferns (sometimes found on rotting logs) with erect *rhizomes*. *Fronde* monomorphic or slightly dimorphic, the *lamina* palmate (in ours) or pinnatifid to bipinnate. *Venation* free or (in ours) reticulate. *Sporangia* distributed along the veins abaxially. *Indusium* lacking.

*Hemionitis* s.l. (i.e., including *Gymnopteris* Bernh.) consists of 6–7 neotropical species, plus a species of the Asian tropics that may not be congeneric. The New World species range from central Mexico and Cuba to Uruguay, with 4–5 occurring in Costa Rica.

##### 1. *Hemionitis palmata* L.

*Petiole of sterile fronds* 3–10(–22) cm long, more or less pubescent. *Sterile lamina* soft-herbaceous, pentagonal, 4–15 cm long and wide, palmately 3–5-lobed, the lobes broad, rounded to acute, coarsely crenate marginally. *Petiole of fertile fronds* 7–28 cm long, the *lamina* more deeply and acutely lobed. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica from 0 to 1,700 m.

A rather weedy species at La Selva, growing along trails and in disturbed open areas on alluvial sites; extremely common in the Arboretum. It is normally terrestrial, but may also grow atop fallen logs.

The palmately lobed, reticulately veined *laminae* easily distinguish *Hemionitis palmata* from all other ferns at La Selva.

#### 18. HYPOLEPIS Bernh.

Coarse, weedy, terrestrial ferns with long-creeping *rhizome*. *Petiole* frequently spinose. *Fronde* large, monomorphic, decomposed, determinate (in ours) or indeterminate. *Venation* free. *Sori* marginal, covered by a modified lobe of the ultimate laminar segment.

In general aspect and soral structure, *Hypolepis* is superficially similar to *Dennstaedtia*, to which it is closely related. The two genera may be easily differentiated at La Selva in that both of our *Hypolepis* species have spinose petioles and rachises. In this regard, fronds of *Hypolepis* closely resemble those of most tree ferns (Cyatheaaceae),

but the latter have round, abaxial sori and erect to arborescent stems.

A pantropical genus of 40–50 species, about 15 of which are American. These range from Central America and south Florida, to southern Chile, and throughout the West Indies. About eight species occur in Costa Rica.

#### KEY TO THE SPECIES

1. Underside of lamina pubescent; rachis and upper part of petiole stramineous, the latter becoming dark purplish-black basally; fronds usually less than 3 m long; plants usually growing in disturbed sites in primary forest. . . . . 1. *H. hostilis*.
1. Underside of lamina glabrous (except for a few hairs along veins); rachis and petiole stramineous to reddened, deeply so toward the base, but never atropurpureous; fronds usually more than 3 m long; plants usually growing in weedy thickets and old fields. . . . . 2. *H. repens*.

#### 1. *Hypolepis hostilis* (Kunze) C. Presl

*Petiole* of fertile fronds often as short as 25–35 cm. *Lamina* 3-pinnate-pinnatifid to 4-pinnate, the largest *pinnae* about 25–70 cm long. Costa Rica to Venezuela and Peru; from 0 to 1,800 m in Costa Rica.

*Hypolepis hostilis* is less common at La Selva than *H. repens*; it is generally a smaller plant, and is more likely to be found in primary forest, though always in disturbed sites (along trails and in light gaps). Despite the specific epithet, it is also the less ferociously armed of our two *Hypolepis* species.

#### 2. *Hypolepis repens* (L.) C. Presl

*Fronds* clambering and subscaudent, to 4–6 m long. *Petiole* to about 2 m long. *Lamina* 3-pinnate-pinnatifid to 4-pinnate-pinnatifid, the largest *pinnae* to 125 cm long and 75 cm wide. Southern Mexico to Bolivia, south Florida, West Indies; from 0 to 1,600 m in Caribbean and southwestern Costa Rica.

Frequent in young secondary growth in alluvial sites (Successional Strips, Sendero El Atajo, La Guaria Annex, etc.), and occasional in upland forest, especially in open, wet areas.

*Hypolepis repens* is a common and familiar fern at La Selva, easily recognized by its thicket-binding habit and spinose frond axes.

#### 19. *LASTREOPSIS* Ching

TINDALE, M. D. 1965. A monograph of the genus *Lastreopsis* Ching. Contr. New South Wales Natl. Herb. 3: 249–339.

Small to medium-sized terrestrial ferns with short-creeping *rhizome*. *Lamina* monomorphic, decomposed, the axes with parallel, adaxial ridges (decurrent on the next lower order) flanking a trichome-filled sulcus. *Venation* free. *Sori* round, abaxial and (in ours) indusiate.

Very similar and probably closely related to *Ctenitis*, but our species much smaller (see Key to the Genera for other differences). *Thelypteris torresiana* might also be confused, but it has glaucous petioles.

A pantropical and Southern Hemisphere genus of 25–35 species, of which 5 are American. The latter range from southern Mexico and Cuba south to southeastern Brazil. Three species occur in Costa Rica.

#### 1. *Lastreopsis exulta* (Mett.) Tind. ssp. *guatemalensis* (Baker) Tind. (=*L. chontalensis* (Fourn.) Lellinger)

*Rhizome* short-creeping. *Petiole* 12–40 cm long. *Lamina* narrowly ovate to deltate, 3-pinnate-pinnatifid, 15–42 cm long, 9–30 cm wide, the basal pair of *pinnae* with enlarged, basal posterior lobes. Southern Mexico to Ecuador; widespread in Costa Rica from 0 to 1,400 m.

Occasional at La Selva in primary forest, where it is nearly restricted to the muddy banks of quebradas. It also grows on the low, rich terrace along the R. Peje near the Cloud Forest Ridge; there, the plants are exceptionally large.

#### 20. *LINDSAEA* J. E. Smith

KRAMER, K. U. 1957. A revision of the genus *Lindsaea* in the New World with notes on allied genera. Acta Bot. Neerl. 6: 97–290.

Small, terrestrial ferns (often growing on logs or roots), the *rhizome* creeping. *Lamina* (in ours) once-pinnate to bipinnate, monomorphic, the *ultimate segments* entire, dimidiate (see under *Adiantum*). *Venation* free (in ours). *Sori* elongate and marginal, indusiate.

Many species of *Lindsaea*, including both of ours, strikingly resemble the unrelated and more familiar maidenhair ferns (*Adiantum*) in their dimidiate ultimate segments. The two genera may be distinguished by the indusia, which open toward the margin in *Lindsaea*, and away from the margin in *Adiantum*. *Didymochlaena* also has dimidiate pinnules, but the sori are borne along the veins. Both of our species of *Lindsaea* are very rare.

A pantropical and Southern Hemisphere genus of 150–200 species, 45 of which are neotropical. Only 6 species occur in Costa Rica.

## KEY TO THE SPECIES

1. Ultimate segments not greatly reduced apically, the terminal one rather large, with large basal lobes, but not deeply pinnatifid; larger ultimate segments more than 1.5 cm long and 6 mm wide. . . 1. *L. lancea*.
1. Ultimate segments strongly reduced to a deeply pinnatifid terminal segment; larger ultimate segments usually less than 1.5 cm long and 6 mm wide. . . . . 2. *L. quadrangularis*.

1. *Lindsaea lancea* (L.) Beddome

*Petiole* 7–53 cm long, yellowish-brown (darker at base). *Lamina* pinnate or bipinnate, 6–50 cm long. *Pinnae* of simply pinnate fronds 7–25 pairs, more or less falcate, up to 3.7 cm long and 1.4 cm wide, the margins entire or (on sterile segments) shallowly sinuate to crenate. *Pinnae* of bipinnate fronds 1–8 pairs, lanceolate, 10–32 cm long, 1–5 cm wide. *Pinnules* mostly subtrapezoidal, 15–25 mm long, 6–11 mm wide, the margins as above. Southern Mexico to Paraguay and the West Indies; from 0 to 1,500 m in Caribbean and southwestern Costa Rica.

*Lindsaea lancea* is quite rare at La Selva, being known only from a few ridges and hilltops in primary forest, in the southern part of the property. Common on the Cloud Forest Ridge. Essentially terrestrial, but often growing on roots or logs. Bipinnate and simply pinnate fronds may occur on the same plant.

Our material belongs in ssp. *lancea*, which has a geographic range coextensive with that of the species.

2. *Lindsaea quadrangularis* Raddi

*Petiole* 11–40 cm long, glossy, quadrangular. *Lamina* bipinnate, 15–50 cm long. *Pinnae* 1–7 pairs, the largest 8.5–25 cm long, 1.5–2.5 cm wide. *Pinnules* subsessile, 8–16 mm long and 3.5–6 mm wide, the margins essentially entire. Southern Mexico to southeastern Brazil, West Indies; from 0 to 1,500 m in Caribbean and southwestern Costa Rica.

Rare at La Selva, mainly on ridges and hilltops in the southern portion of the property; one collection is from the edge of an open marsh along the Camino Experimental Sur. Nominally terrestrial, though frequently growing on roots, stumps, etc.

Our plants represent ssp. *subalata* Kramer, which occurs from southern Mexico to Colombia, and in Cuba.

21. *LOMARIOPSIS* Fée

UNDERWOOD, L. M. 1906. American ferns—VII. Bull. Torrey Bot. Club 33: 591–605.

Ours appressed-climbing understory trunk epiphytes with long-creeping *rhizome*. *Fronde* dimorphic, once-pinnate, the pinnae articulate with the rachis. *Venation* free. *Sporangia* completely covering the fertile lamina abaxially.

The above characteristics serve to distinguish our two species of *Lomariopsis* from all other ferns at La Selva. *Bolbitis nicotianifolia* is similar in habit, but has reticulate venation.

*Lomariopsis* is a pantropical genus of 40–45 species. About 15–20 species inhabit the Americas, ranging from southern Mexico and south Florida to southeastern Brazil, and throughout the West Indies. Four species are attributed to Costa Rica.

## KEY TO THE SPECIES

1. Pinnae more than 15 pairs, more than 3 cm wide and 12 cm long; rachis not winged; rare, except in abandoned cacao. . . . . 1. *L. japurensis*.
1. Pinnae more than 15 pairs, less than 3 cm wide and 12 cm long; rachis narrowly winged; common in primary forest. . . . . 2. *L. vestita*.

1. *Lomariopsis japurensis* (Martius) J. Smith

*Petiole of sterile frond* 18–30 cm long, scaly toward base. *Sterile lamina* about twice as long, to 30 cm wide, once-pinnate, broadly lanceolate, the rachis unwinged. *Sterile pinnae* 5–13 pairs, mostly short-stalked, the largest ones 15–20 cm long, 4–6 cm wide. *Petiole of fertile frond* 10–30 cm long. *Fertile lamina* 12–26 cm wide, the *pinnae* 8–15 pairs, 8–17 cm long and 1–1.7 cm wide. Guatemala and Belize to Bolivia, Trinidad and the Guianas; from 0 to 600 m in Costa Rica, on both coasts.

Rather uncommon at La Selva, usually in cacao groves or older secondary growth on alluvial sites. A trunk epiphyte, usually fertile about 1.5–2.5 m above the ground.

*Lomariopsis japurensis* would never be confused with *L. vestita*, but it does bear a striking resemblance to *Polybotrya cervina*, under which name it is pictured in Tryon and Tryon (1982, figure 80.1). The latter, however, is a short-stemmed plant usually growing atop rotting logs, and has bipinnate fertile fronds.

2. *Lomariopsis vestita* Fourn.

*Petiole of sterile frond* 1–10 cm long, scaly. *Sterile lamina* 23–70 cm long, 6–20 cm wide, once-pinnate, oblanceolate, the rachis winged. *Pinnae* 20–35 pairs, subsessile, the larger ones 3–10 cm long, 0.9–2.0 cm wide, lanceolate, truncate to cordate basally, the margins entire to minutely toothed. *Petiole of fertile frond* 4–17 cm



long. *Fertile lamina* to 16 cm wide, the largest pinnae 3–8 cm long and 1–3 mm wide. Southern Mexico to Venezuela; widespread in Costa Rica from 0 to 1,500 m.

Appressed-climbing on the stems of understory treelets in primary forest, generally becoming fertile at a height of 1–2 m. One of the commonest ferns at La Selva.

The name *Lomariopsis vestita* has generally been treated as a synonym of *L. fendleri* D. Eaton, however recent observations suggest that the two may be distinct.

## 22. LONCHITIS L.

TRYON, R. 1962. Taxonomic fern notes. III. Contr. Gray Herb. 191: 91–107.

Terrestrial ferns with short-creeping *rhizome*. *Fronde* monomorphic, pinnate-pinnatifid. *Venation* essentially free (in ours). *Sori* elongate and marginal, indusiate.

Similar in most respects to *Pteris*, though not closely related. *Lonchitis hirsuta* can be easily distinguished from our *Pteris* species by its soft foliage, succulent petioles and abundant whitish pubescence, especially on the petioles and rachis.

A genus of just two species, one of tropical Africa and Madagascar, the other ranging from southern Mexico and Cuba to Bolivia.

### 1. *Lonchitis hirsuta* L.

*Petiole* 20–90 cm long, hollow, hirsute. *Lamina* to 30–200 m long and to 1 m wide, bipinnate-pinnatifid (or the basal pinnae further divided), deltate-ovate, conspicuously whitish-pubescent. *Pinnae* 7–10 pairs. *Pinnules* 2.5–12 cm long (the basal ones much longer), 1–3 cm wide. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica from 0 to 2,000 m.

Occasional at La Selva in cacao groves and old secondary growth on alluvial sites, often near creeks or drainage ditches.

## 23. NEPHROLEPIS Schott

NAUMAN, C. E. 1985. A systematic revision of the neotropical species of *Nephrolepis* Schott. Ph.D. thesis, University of Tennessee, Knoxville.

Epiphytic or occasionally terrestrial ferns, the *rhizome* erect or short-creeping, often sending out long runners. *Lamina* monomorphic, once-pinnate, narrowly lanceolate and often pendent, ours with 40 or more pairs of articulate *pinnae*. *Venation* free. *Sori* round, abaxial, in a single row on either side of the costa, with a conspicuous lunate to orbicular *indusium*.

A pantropical genus of 20–30 species, 6–7 of

which are native in the Americas. The latter range from central Mexico, south Florida and Bermuda, to southeastern Brazil, and throughout the West Indies. Six species occur in Costa Rica. At La Selva, *Nephrolepis* can only be confused with *Cyclopetis*, which has two rows of sori on either side of the costa.

### KEY TO THE SPECIES

1. Pinnae cordate basally, at least on one side, the basal lobes (or one of them) overlapping the rachis; sori reniform or semicircular; fronds often more than 2 m long, long-pendulous. . . . 3. *N. pendula*.
1. Pinnae cuneate or truncate basally, the lobes not or scarcely overlapping the rachis; sori circular; fronds rarely more than 2 m long.
  2. Rachis conspicuously scurfy with dark brown, hair-like scales; pinnae glabrous below, the margins entire except toward the apex, the basal lobe broadly triangular, acute. . . . . 4. *N. rivularis*.
  2. Rachis not scurfy or, if so, with very pale brownish scales; pinnae pubescent or filiform-scaly below, the margins serrate or crenate to the base; basal lobe, if acute, narrower.
    3. Petiole scales spreading, narrow, light brown; pinnae usually pubescent below, the basal lobe usually broad and obtuse to obsolete; common. . . . . 1. *N. biserrata*.
    3. Petiole scales appressed, broad, dark brown with narrow, pale margins; pinnae more or less filiform-scaly below, the basal lobe long, narrow and acute; uncommon. . . . . 2. *N. multiflora*.

### 1. *Nephrolepis biserrata* (Sw.) Schott

Terrestrial or epiphytic. *Petiole* 5.5–60 cm long. *Lamina* erect to pendulous, 23–200 m long or more, broadly linear, (4–)14–30 cm wide. *Pinnae* numerous, short-stalked or sessile, the larger ones (2–)6.5–16 cm long and (0.45–)1.1–2.4 cm wide, crenate to serrate marginally, the tissue subglabrous to copiously pubescent. *Indusium* circular. Southern Mexico to Brazil, south Florida, West Indies; Africa, Asia, Oceania; from 0 to 400 m in Caribbean and southwestern Costa Rica.

Though usually found on alluvial sites at La Selva, *Nephrolepis biserrata* is perhaps our most ecologically versatile fern. It is most commonly seen as a terrestrial plant or stump or low trunk epiphyte in well-lit situations, such as clearings, young secondary growth and open marshes. Plants growing rather high up on trunks of *Astrocaryum alatum* Loomis in primary swamp forest (Plot II) appear very different in having pendulous fronds that are abundantly pubescent.

### 2. *Nephrolepis multiflora* (Roxb.) Jarrett ex C. Morton

Terrestrial or epiphytic. *Petiole* 5–66 cm long. *Lamina* to 1 m long or more, lance-linear, 7–20 cm broad. *Pinnae* numerous, sessile, the larger ones 5–12 cm long and 0.6–1.4 cm wide, crenate to serrate marginally. *Indusium* circular. Indigenous to India and tropical Asia, but widely naturalized in the New World from Guatemala to Brazil, and in south Florida and the West Indies; from 0 to 400 m in Caribbean and southwestern Costa Rica.

Occasional at La Selva in abandoned pastures and secondary growth, less frequently in disturbed areas (such as trail edges) in primary forest.

### 3. *Nephrolepis pendula* (Raddi) J. Smith

Epiphytic (at La Selva), the fronds pendent. *Petiole* 4–30 cm long. *Lamina* 0.35–3 m long, 3–11.5 cm wide. *Pinnae* sessile, the larger ones 1.4–6 cm long, 4–12 mm wide, rounded to subcordate basally on the posterior side, the margins subentire to shallowly crenate. *Indusium* lunate or reniform. Southern Mexico to Bolivia; widespread in Costa Rica from 0 to 1,800 m.

Occasional at La Selva as a trunk epiphyte, usually growing at 4–6 m or higher in cacao or old secondary forest on alluvial sites.

### 4. *Nephrolepis rivularis* (Vahl) Mett. ex Krug

Epiphyte (at La Selva). *Petiole* 12–50 cm long. *Lamina* linear, 50–105 cm long, 5–10 cm wide at widest point, the pinnae numerous. *Pinnae* sessile, the largest ones 2.5–6 cm long and 5–9 mm wide, strongly inaequalateral at base, the margins subentire to shallowly crenulate or bluntly serrate. *Indusium* circular. Southern Mexico to Peru and the Guianas, West Indies; from 0 to 1,300 m on the Caribbean slope of Costa Rica.

Scattered in upland primary forest at La Selva, frequently low on trunks in the vicinity of light-gaps; also in the canopy.

## 24. OLEANDRA Cav.

SCAMMAN, E. 1961. The genus *Oleandra* of Costa Rica. *Rhodora* 63: 335–340.

Epiphytic ferns with creeping, conspicuously scaly *rhizome*. *Fronds* monomorphic (in ours). *Petiole* conspicuously articulate above the *rhizome*. *Lamina* simple, entire, lanceolate. *Venation* free. *Sori* round, abaxial, clearly indusiate.

*Oleandra* is one of our most distinctive fern genera. It might be confused with some species of *Polypodium* (subgenus *Campyloneurum*), but

those have reticulate venation and exindusiate sori.

A pantropical genus of about 40 species, ranging in the New World from Chiapas and Cuba to southeastern Brazil. Four species occur in Costa Rica.

### 1. *Oleandra articulata* (Sw.) C. Presl

*Rhizome* appressed to divergent, densely covered with spreading, reddish-brown scales. *Petiole* 5–28 cm long, conspicuously articulate 0.5–6 cm above the *rhizome*. *Lamina* narrowly lanceolate, 15–55 cm long and 2.7–8 cm wide, bright green, glossy and somewhat papery in texture, the midrib scaly below. *Sori* concentrated near the midrib, conspicuously indusiate. Southern Mexico to Bolivia, West Indies; from 0 to 1,000 m in Costa Rica, on the Caribbean slope and Cocos Island.

Occasional at La Selva as a trunk epiphyte, mainly in upland primary forest.

## 25. PITYROGRAMMA Link

TRYON, R. 1962. Taxonomic fern notes. II. *Pityrogramma* (including *Trismeria*) and *Anogramma*. *Contr. Gray Herb.* 189: 52–76.

Terrestrial, usually weedy ferns with erect *rhizome*. *Lamina* (in ours) monomorphic, decompound and covered below with a chalky white or yellowish indumentum. *Venation* free. *Sporangia* inconspicuous, borne individually along the veins.

A genus of 16–20 species, with 4–5 in Africa and Madagascar, one in the western United States and the rest in the neotropics. *Pityrogramma* ranges in the Americas from the Pacific northwestern United States to central Argentina. Seven species occur in Costa Rica (including *Trismeria* Fée). Our species are instantly recognizable by the usually chalky-white undersurface of the lamina.

### KEY TO THE SPECIES

1. Posterior and anterior pinnules of basal pinnae subequal; pinnules often spreading acutely; common. . . . . 1. *P. calomelanos*.
1. Posterior pinnules of basal pinnae significantly longer than anterior pinnules; pinnules spreading at nearly right angles; to be expected. . . . . 2. *P. tartarea*.

### 1. *Pityrogramma calomelanos* (L.) Link (=*P. ebenea* (L.) Proctor)

*Petiole* 9.5–46 cm long, glossy and blackish. *Lamina* lanceolate to ovate, 11.5–50(–95) cm

long, 4.5–20(–30) cm wide, bipinnate to bipinnate-pinnatifid, bright to dark green above, white to cream or (rarely, at La Selva) yellow below. Southern Mexico to Argentina, south Florida, West Indies; introduced in Africa, tropical Asia, Oceania; widespread in Costa Rica, from 0 to 1,300 m.

A common weedy fern in clearings and disturbed sites at La Selva, usually near the rivers or in alluvial areas, but occasionally in upland forest. Individuals with white and yellowish lower leaf surfaces may occur intermixed in the same population, as along the R. Peje.

## 2. *Pityrogramma tartarea* (Cav.) Maxon

*Petiole* 9.5–70 cm long, stout, atropurpureous. *Lamina* broadly lanceolate, pinnate-pinnatifid to (basally) bipinnate, 11.5–80 cm long, 3.5–35 cm wide, white-farinoso below. Mexico to Bolivia, West Indies; widespread in Costa Rica from (0 to) 600 to 1,900 m.

There are to date no specimens of *Pityrogramma tartarea* from La Selva, however it has been collected in the immediate vicinity (*Biolley* 7506, CR; Puerto Viejo de Sarapiquí) and should be sought, especially in disturbed areas along the rivers.

According to some interpretations, the name *Pityrogramma ebenea* (L.) Proctor refers to this species rather than *P. calomelanos*, in which case it has priority over *P. tartarea*.

## 26. POLYBOTRYA Humb. & Bonpl. ex Willd.

MORAN, R. C. 1986. The neotropical fern genus *Olfersia*. Amer. Fern J. 76: 161–178.

———. 1987. Monograph of the neotropical fern genus *Polybotrya* (Dryopteridaceae). Bull. Illinois Nat. Hist. Surv. 34: 1–138.

Plants terrestrial, growing atop logs or appressed-climbing on trunks. *Rhizome* coarse, scaly, short- to long-creeping. *Fron*ds dimorphic, the sterile ones once-pinnate to decompose, the fertile ones bipinnate to decompose. *Venation* essentially free (in ours). *Sporangia* mostly covering the abaxial side of fertile laminae. *Indusium* absent.

These are our only ferns with dimorphic fronds in which the fertile laminae are extensively divided (bipinnate to decompose). Ignoring the habitally and morphologically aberrant *P. cervina*, they are also the only epiphytic ferns at La Selva with large, decompose laminae, and thus are not to be confused with anything else even in sterile condition.

*Polybotrya* is a neotropical genus of 35 species,

ranging from southern Mexico (Chiapas) and Cuba to southeastern Brazil. It is most diverse in the Andes. Seven species occur in Costa Rica.

### KEY TO THE SPECIES

1. Sterile lamina simply pinnate, with a conform terminal pinna; pinnae with a continuous submarginal vein; fertile lamina bipinnate; plants terrestrial or on logs, the rhizome short-creeping. 3. *P. cervina*.
1. Sterile and fertile lamina decompose (more than bipinnate), the apex pinnatifid; submarginal vein lacking; fertile lamina subbipinnate to decompose; usually appressed-climbing trunk epiphytes, the rhizome long-creeping.
  2. Scales of rhizome reddish-brown, closely appressed; rachis of sterile fronds pubescent; costae conspicuously pilose, the costules and smaller veins pubescent as well; ultimate segments of fertile fronds lance-caudate, the apical entire portions to more than 4 cm long. . . . . 2. *P. caudata*.
  2. Scales of rhizome brown, spreading; rachis of sterile fronds essentially glabrous, except toward the apex; costae and costules pilosulous, the smaller veins glabrous; ultimate segments of fertile fronds round to somewhat caudate, the apical entire portion never so long.
    3. Sterile lamina bipinnate-pinnatifid, some basal pinnules sometimes with a few free lobes, but these then entire to apically denticulate; fertile lamina tripinnate, the ultimate segments linear; rachis and costae of fertile fronds scaly, otherwise glabrous except in the groove above; occasional. . . . . 4. *P. osmundacea*.
    3. Sterile lamina largely tripinnate, the ultimate segments crenate-serrate to lobed; fertile lamina 3–4-pinnate, the ultimate segments suborbicular; rachis and costae of fertile fronds abundantly pubescent as well as scaly; rare. . . . . 1. *P. alfredii*.

## 1. *Polybotrya alfredii* Brade (= *P. gracilis* Brade)

Epiphyte. *Petiole* 12–26 cm long (–36 cm on fertile fronds). *Sterile lamina* oblong-lanceolate, about 45–65 cm long, 35–40 cm wide. *Largest pinnae* 20–30 cm long and 9–16 cm wide. *Fertile lamina* smaller, the pinnae 15–18 cm long. Nicaragua to Bolivia; from 0 to 1,900 m in Costa Rica.

Known from La Selva by a single collection, from along the Q. El Saltito at about Line 2400.

## 2. *Polybotrya caudata* Kunze (= *P. costaricensis* Brade; *P. villosula* Christ)

Epiphyte. *Petiole* 25–70 cm long. *Sterile lamina* to 1.3 m long and 30–60 cm wide, the axes conspicuously pubescent. *Largest pinnae* 20–40

cm long, 7–20 cm wide, the segment margins minutely ciliate. *Fertile lamina* similar in size, the *pinnules* to about 10 cm long, pinnatifid to linear and entire. Southern Mexico to Bolivia, Trinidad and the Guianas; from 0 to 1,500 m in Caribbean and southwestern Costa Rica.

Common throughout in primary forest, the most abundant of our epiphytic *Polybotrya* species. The plants may climb to as much as 3–4 m above the ground.

3. ***Polybotrya cervina* (L.) Kaulf.**  
(=*Olfersia cervina* (L.) Kunze)

Growing atop logs, or (rarely, at La Selva) terrestrial. *Petiole of sterile frond* 20–55 cm long. *Sterile lamina* 30–85 cm long, 20–35 cm wide, narrowly oblong, once-pinnate. *Sterile pinnae* 4–12 pairs, lanceolate, the largest 14–25 cm long, 3–7 cm wide, subentire. *Veins* numerous, closely parallel, joined apically by a submarginal connecting vein. *Petiole of fertile frond* 45–90 cm long. *Fertile lamina* bipinnate, the *pinnae* ascending, 8–21 cm long and 1–3 cm wide; lobes linear, 4–10 mm long. Southern Mexico (Oaxaca) to Bolivia and southeastern Brazil, West Indies; from 0 to 1,100 m in Caribbean and southwestern Costa Rica.

Common throughout, in primary forest. Nearly always seen growing atop rotting logs in or near older light gaps; this and *Asplenium cirrhatum* are our only ferns that consistently exploit this habitat. On the Cloud Forest Ridge, just outside La Selva proper, *P. cervina* is commonly “terrestrial” on springy, root-laden “soil.”

*Polybotrya cervina* differs from the other species in the genus in its conform terminal *pinnae*, in venation pattern and in details of stem anatomy (Moran, 1986); it is sometimes segregated into its own genus, *Olfersia*. *P. cervina* bears a strong superficial resemblance to *Lomariopsis japurensis*.

4. ***Polybotrya osmundacea* Humb. & Bonpl. ex Willd.**

Epiphyte. *Petiole* 15–40 cm long. *Sterile lamina* to 1 m long, 30–50 cm wide, ovate to deltate. Largest *pinnae* about 25–50 cm long, 9–25 cm wide, the segment margins glabrous. *Fertile lamina* similar in size. Guatemala and Belize to Bolivia, West Indies; from 0 to 1,500 m in Caribbean and southwestern Costa Rica.

Occasional in primary forest at La Selva, though less common than *P. caudata* and generally occurring in wetter places (swamp forest, along sluggish streams, etc.). It may not climb as high as *P. caudata*, and some fertile adults are virtually terrestrial—i.e., with the elongate rhizome barely rising above the ground at the base of a trunk.

27. **POLYPODIUM L.**

EVANS, A. M. 1969. Interspecific relationships in the *Polypodium pectinatum-plumula* complex. Ann. Missouri Bot. Gard. 55: 193–293.

LELLINGER, D. B. 1972. A revision of the fern genus *Niphidium*. Amer. Fern J. 62: 101–120.

———. 1988. Some new species of *Campyloneurum* and a provisional key to the genus. Amer. Fern J. 78: 14–35.

PRICE, M. G. 1983. *Pechuma*, a new tropical American fern genus. Amer. Fern J. 73: 109–116.

SEYMOUR, F. C. 1975. *Polypodium* in Nicaragua. Phytologia 31: 129–192.

Epiphytic ferns, the *rhizome* very short- to long-creeping. *Petiole* obscurely articulate with the rhizome. *Lamina* monomorphic or occasionally weakly dimorphic, simple and narrowly linear to oblanceolate or ovate, or pinnately lobed to pinnatifid (but ours always with the margins entire). *Venation* free to reticulate. *Sori* round, abaxial, exindusiate.

Although species of *Polypodium* tend to be rather nondescript, most are easily placed by their epiphytic habit, entire (ignoring pinnation) leaf margins and round, exindusiate sori. Elsewhere the genus can be easily confused with *Grammitis*, but the two La Selva species of the latter genus are distinctive.

*Polypodium* is frequently divided into several segregate genera. The present treatment follows Stolze (1981) and Proctor (1985), among recent authors, in treating the latter as subgenera of a broadly circumscribed *Polypodium*. Some of these subgenera, such as *Campyloneurum*, are reasonably well defined; others, particularly *Polypodium*, are probably polyphyletic (see Price, 1983). As a matter of convenience, the La Selva species of *Polypodium* s.l. are keyed artificially, but grouped by subgenus in the text.

*Polypodium* s.l. is a cosmopolitan genus of 200–225 species, most of them tropical and about 180 American. The genus virtually spans the New World, from Alaska and southern Greenland to the southern tip of South America. About 75 species are known from Costa Rica.

## KEY TO THE SPECIES

1. Lamina simple, entire to shallowly sinuate.
2. Rhizome long-creeping; lamina rounded to cuneate, acute or short-attenuate basally, usually with a definite petiole or, if not, the fronds less than 10 cm long; lamina never more than 8 cm wide.
3. Laminae, at least the larger ones, more than 3 cm wide; uncommon. . . . . 4. *P. sphenodes*.
3. Lamina always less than 3 cm wide; abundant.
4. Laminae, at least the larger ones, more than 10 cm long, abundantly provided with circular, peltate scales. . . . . 9. *P. percussum*.
4. Lamina usually less than 10 cm long, lacking circular, peltate scales (caution: may possess filiform scales with broadened, peltate bases).
5. Lamina scaly, at least along the margins; fronds dimorphic, the fertile ones linear, the sori overlapping the margin. . . . . 5. *P. ciliatum*.
5. Lamina glabrous; fronds only slightly dimorphic, the sori not overlapping the margins of the fertile fronds. . . . . 6. *P. lycopodioides*.
2. Rhizome short-creeping; lamina long-attenuate basally, the petiole not evident or very short or, if longer, the lamina more than 8 cm wide; lamina never less than 10 cm long.
6. Largest laminae more than 5 cm wide; common.
7. Lamina dotted below with minute whitish encrustations; sori in a single row between the costae. . . . . 7. *P. crassifolium*.
7. Lamina essentially glabrous below; sori in two or more rows between the costae. . . . . 2. *P. latum*.
6. Largest laminae less than 5 cm wide; rare.
8. Lamina very narrow, less than 2 cm wide, glabrous, the margins revolute; sori in a single row on either side of the midvein. . . . . 1. *P. angustifolium*.
8. Lamina broader, more than 2 cm wide, covered with minute trichomes, the margins plane; sori in 3-5 rows on either side of the midvein. . . . . 3. *P. occultum*.
1. Lamina pinnate or deeply and regularly pinnatifid.
9. Laminar surface densely whitish-scaly below and, to a lesser degree, above. . . . . 11. *P. furfuraceum*.
9. Laminar surface never scaly.
10. Small plants, the largest laminae (at La Selva) less than 25 cm long; venation free, no areolae present along the costae. . . . . 12. *P. hygrometricum*.
10. Larger plants, the largest laminae more than 25 cm long; venation reticulate or free.
11. At least the basal 3-4 pairs of pinnae free, not connected by wings of laminar tissue.
12. Pinnae uniformly pubescent on both surfaces, not contracted basally; scales of rhizome iridescent dark brown. . . . . 10. *P. dissimile*.
12. Pinnae glabrous, or pubescent only near the margins, constricted basally; scales of rhizome reddish.
13. Terminal pinnae gradually reduced to a pinnatifid apex; venation free; sori in one row on either side of the costae; understory trunk epiphyte. . . . . 16. *P. sororium*.
13. Terminal pinna entire, resembling the lateral pinnae; venation reticulate; sori in 2-3 rows on either side of the costae; canopy epiphyte. . . . . 17. *P. triseriale*.
11. No pinnae truly free, connected to adjacent pinnae on the same side of the rachis by laminar wings.
14. Lamina strongly glaucous, the larger pinnae more than 15 cm long and more than 2 cm wide. . . . . 8. *P. pseudoaureum*.
14. Lamina green, the pinnae less than 15 cm long and 2 cm wide.
15. Basal pinnae abruptly and drastically reduced, often to mere nubs; venation free; rhizome scales hairlike, spreading. . . . . 15. *P. pectinatum*.
15. Basal pinnae not reduced, or only slightly; venation reticulate, the areoles with free included veinlets; rhizome scales circular, appressed.
16. Rhizome scales remote; larger pinnae horizontally spreading or curved at tips, less than 5 cm long; rachis generally pilose below (rarely glabrous); petiole less than half as long as lamina. . . . . 13. *P. loriciforme*.
16. Rhizome scales densely covering the rhizome; larger pinnae strongly curved forward, more than 5 cm long; rachis glabrous or minutely pubescent; petiole more than half as long as lamina. . . . . 14. *P. maritimum*.

## Subgenus CAMPYLONEURUM

1. **Polypodium angustifolium Sw.**  
(=*Campyloneurum angustifolium* (Sw.) Fée)

Rhizome short-creeping. Petiole usually less than 2 cm long, occasionally longer. Lamina lin-

ear, 15-70 cm long, 0.3-1.5 cm wide, the margins entire. Venation reticulate. Southern Mexico to Argentina, south Florida, West Indies; wide-spread in Costa Rica from 0 to 2,200 m (excluding *P. amphostenon* Kunze ex Klotzsch as a separate species).

Occasional at La Selva on alluvial sites, usually

as a canopy epiphyte on emergent trees; most commonly found on downfalls.

2. **Polypodium latum** (T. Moore) T. Moore ex Sodiro  
(=*Campyloneurum latum* T. Moore)

*Rhizome* short-creeping, the fronds clustered. *Petiole* usually light brown, 4–23 cm long. *Lamina* narrowly elliptic to oblanceolate, 45–115 cm long, 5–13 cm wide, the margins subentire to undulate. *Venation* reticulate. Mexico to Uruguay, Florida, West Indies; from 0 to 1,300 m in Caribbean and southwestern Costa Rica.

Common and conspicuous as a trunk or crotch epiphyte on alluvial sites, sometimes growing quite low (to about 1.5 m above the ground) on cacao trees, etc.

It is exasperatingly difficult to decide on the proper specific epithet for what is perhaps the most abundant and conspicuous *Polypodium* at La Selva. Although representing but a single species, our material has been variously identified (sometimes by the same authority) as either *P. latum*, *P. brevifolium* Link or *P. phyllitidis* L. Inasmuch as La Selva material consistently comes out to *P. latum* in keys purporting to separate that species from either or both of the other two, we have opted for this name. This should be regarded as an ad hoc and highly tentative decision, however, since *Polypodium latum* is considered conspecific with *P. brevifolium* by some authorities, and with *P. phyllitidis* by others. Since both of the latter names have priority over *P. latum*, either could replace it in the appropriate scenario.

3. **Polypodium occultum** Christ  
(=*Campyloneurum occultum* (Christ) L. D. Gómez)

*Rhizome* short-creeping, the fronds crowded. *Petiole* obsolete or to 4.5 cm long. *Lamina* oblanceolate, 10–40 cm long, 1.5–5 cm wide, with minute whitish trichomes (at least below), the margins subentire. *Venation* reticulate. Southern Mexico to Ecuador; from 0 to 1,500 m in Caribbean and southwestern Costa Rica.

Occasional, mostly as a low trunk epiphyte on rather large trees on alluvial sites; most common in primary swamp forest.

4. **Polypodium sphenodes** Kunze ex Klotzsch  
(=*P. wercklei* Christ; *Campyloneurum sphenodes* (Kunze ex Klotzsch) Fée)

*Rhizome* slender, long-creeping. *Petiole* 1–14 cm long. *Lamina* narrowly elliptical to lanceolate, (6.5–)13–34 cm long and 1.5–8 cm wide,

long-acuminate apically and attenuate at the base, the margins subentire to coarsely crenate or sinuate. *Venation* reticulate. Costa Rica to Brazil; widespread in Costa Rica from 0 to 1,900 m.

Occasional as a branch or trunk epiphyte in the understory, usually on alluvial sites: primary swamp forest, cacao, old secondary forest, etc.

Subgenus MICROGRAMMA

5. **Polypodium ciliatum** Willd.  
(=*Microgramma reptans* (Cav.) A. R. Smith)

*Rhizome* long-creeping, abundantly scaly. *Fron*ds somewhat dimorphic. *Petiole of sterile fronds* obsolete or to 3.5 mm long. *Sterile lamina* ovate to narrowly elliptic or oblong, 1.2–5 cm long and 0.8–1.5 cm wide, both surfaces with appressed, filiform scales, the margins ciliate with same. *Venation* reticulate, the areoles in a single row along the costa. *Petiole of fertile fronds* to about 1 cm long. *Fertile lamina* linear, 2–6 cm long and 1.5–2.5 mm wide, the sori projecting beyond the margins. Southern Mexico to Bolivia, Trinidad; widespread from 0 to 1,800 m in Costa Rica.

Very common at La Selva as a canopy branch epiphyte, mainly in secondary growth and alluvial forest; also on planted *Citrus*, etc.

Lellinger (1989) attributes the very similar *P. blandulum* Christ (as *Microgramma tecta* (Kaulf.) Alston) to La Selva, but cites no specimen.

6. **Polypodium lycopodioides** L.  
(=*Microgramma lycopodioides* (L.) Copel.)

*Rhizome* slender, long-creeping, with appressed to spreading scales. *Fron*ds somewhat dimorphic, the petioles obsolete or to 3 mm long. *Sterile lamina* lanceolate, 2–8.5 cm long and 0.9–2 cm wide, glabrous, the margins entire. *Venation* reticulate. *Fertile lamina* 1.5–10(–14.5) cm long, 0.5–1.7 cm wide, the sori impressed. Southern Mexico to Bolivia, West Indies; Africa; widespread in Costa Rica from 0 to 2,700 m.

A canopy branch and twig epiphyte; common throughout, in primary forest, secondary growth and planted groves.

Subgenus NIPHIDIUM

7. **Polypodium crassifolium** L.  
(=*Niphidium crassifolium* (L.) Lellinger)

*Rhizome* short-creeping. *Petiole* 0.5–20 cm long. *Lamina* lanceolate to oblanceolate, (14–)25–105 cm long, (2.2–)5–18 cm wide, dark green above, paler beneath with minute whitish encrustations, acute to rounded apically, attenuate at the base, the margins entire, usually revolute. *Venation* reticulate. Southern Mexico to Bolivia,

West Indies; throughout Costa Rica, from 0 to 2,100 m.

Uncommon at La Selva in alluvial sites, such as along rivers and in swamp forest, and along quebradas in upland primary forest; mainly a trunk epiphyte, to 3–5 m above the ground on large trees.

*Polypodium crassifolium* is superficially rather similar to *P. latum*, although included in a different subgenus; we have seen herbarium specimens misdetermined by authorities who would place the two species in separate genera!

#### Subgenus PHLEBODIUM

8. ***Polypodium pseudoaureum* Cav.**  
(=*Phlebodium pseudoaureum* (Cav.) Lellinger)

*Rhizome* coarse, densely covered with rusty scales. *Petiole* 15–65+ cm long, glossy. *Lamina* deeply pinnatifid, ovate, 20–100 cm long, 15–50 cm wide, usually glaucous (at least below). *Segments* 5–16 pairs, lanceolate, 9–35 cm long, 1–5 cm wide. *Venation* reticulate. Northern Mexico to Argentina, south Florida, West Indies; widespread in Costa Rica from 0 to 2,300 m.

A common and conspicuous trunk or bough epiphyte at La Selva, usually in alluvial sites; most commonly seen on trunks of pejibaye trees.

Tryon and Tryon (1982) do not recognize *Phlebodium* as distinct from *Polypodium* s. str.

#### Subgenus PLEOPELTIS

9. ***Polypodium percussum* Cav.**  
(=*Pleopeltis percussa* (Cav.) Hook. & Grev.)

*Rhizome* slender, long-creeping, scaly. *Petiole* 0.5–6 cm long, scaly. *Lamina* narrowly elliptic, 7–31 cm long and 0.9–3.5 cm wide (the fertile ones generally longer and narrower), acuminate to caudate apically, cuneate at the base, bearing minute, peltate scales below, the margins entire. *Venation* reticulate. Southern Mexico to Bolivia; widespread in Costa Rica from 0 to 1,500 m.

Common throughout, especially in alluvial sites but also in upland primary forest. A canopy branch or twig epiphyte.

#### Subgenus POLYPODIUM

10. ***Polypodium dissimile* L.**  
(=*P. chnoodes* Sprengel; *Goniophlebium chnoodes* (Sprengel) Fée)

*Rhizome* stout, short-creeping, densely covered with dark brown, iridescent scales. *Petiole* 6–25 cm long, pubescent at least apically. *Lamina* oblong to lanceolate, 20–90 cm long, 8–25

cm wide, soft-herbaceous, pubescent throughout, pinnate, the pinnae opposite, 15–32 pairs. Larger *pinnae* 4–12 cm long, 0.8–1.8 cm wide, lanceolate, the margins subentire. *Venation* reticulate. Southern Mexico to Venezuela, West Indies; from 0 to 1,500 m in Costa Rica, on both slopes.

A trunk epiphyte, common at La Selva in alluvial sites (cacao, pejibaye, Arboretum) and occasional along quebradas in upland primary forest.

11. ***Polypodium furfuraceum* Schldl. & Cham.**

*Rhizome* rather stout, short- to long-creeping. *Petiole* 2–13.5 cm long, densely scaly. *Lamina* 5–30 cm long, 1.5–5.5(–8.5) cm wide, deeply pinnatifid, lanceolate, coriaceous, densely covered (at least below) with small, whitish to brownish, appressed scales. *Segments* numerous, linear, 1.2–4 mm wide, the margins entire. *Venation* free. Southern Mexico to Bolivia; widespread in Costa Rica from 0 to 2,100 m.

A distinctive species, common throughout, mostly as a canopy branch epiphyte in alluvial and upland primary forest; most frequently encountered on downfalls, but grows low down on *Citrus*, pejibaye, etc.

12. ***Polypodium hygrometricum* Splitg.**  
(=*Pecuma hygrometrica* (Splitg.) M. Price)

*Rhizome* long-creeping. *Petiole* 1–4 cm long, pubescent. *Lamina* elliptic to lanceolate, pinnatifid, 4.5–15(–40) cm long and 2–6 cm wide. *Segments* 8–28 pairs, 2.5–6(–16) mm wide, the margins subentire. *Venation* reticulate, the areolae in a single series. Southern Mexico to Bolivia; from 0 to 850 m in Costa Rica.

Occasional in disturbed areas on alluvium; locally abundant as a trunk epiphyte on cacao trees and on large trees along the rivers, as at Rafael's House; it may also grow epilithically on concrete stairs, etc.

13. ***Polypodium loriforme* Rosenstock**  
(=*P. subviride* Lellinger)

*Rhizome* long-creeping, loosely scandent or appressed, the fronds distant. *Petiole* 2.5–9.5 cm long, marginate to narrowly erect-winged. *Lamina* narrowly lanceolate, deeply pinnatifid, 14–50 cm long, 3.5–10 cm wide. *Segments* about 27–50 pairs, straight or somewhat falcate, the largest 2–5 cm long and ca. 4.5–8.5 mm wide. *Venation* reticulate. Costa Rica to Colombia; from 0 to 1,500 m on the Caribbean slope of Costa Rica.

Fairly common in upland primary forest and old secondary growth; usually seen in well-lit spots in the understory, as on treelets arching over quebradas.

*Polypodium loriciforme* is usually easily identifiable at La Selva by the conspicuously pilose (with trichomes to more than 1 mm long) undersurface of the rachis. Plants in certain populations (along Q. El Taconazo at Sendero El Surá; along R. Sarapiquí below Sendero Ribeño) have perfectly glabrous rachises, but are otherwise indistinguishable from the usual form.

#### 14. *Polypodium maritimum* Hieron.

*Rhizome* stout, long-creeping, the fronds distant. *Petiole* 10–50 cm long. *Lamina* lanceolate, deeply pinnatifid or subpinnate, 20–70 cm long and 10–28 cm wide. *Pinnae* about 15–50 pairs, more or less falcate, the largest ones 6–14 cm long, 1–2 cm wide. *Venation* reticulate. Nicaragua to Ecuador; from 0 to 1,400 m on the Caribbean slope of Costa Rica.

Occasional trunk or bough epiphyte at La Selva, usually on large trees on alluvium; rare in upland primary forest.

#### 15. *Polypodium pectinatum* L. (=*Pecluma pectinata* (L.) M. Price)

*Rhizome* long-creeping. *Petiole* 2.5–12 cm long. *Lamina* narrowly linear to lanceolate, 20–90 cm long, 4.5–10.5 cm wide, deeply pinnatifid. *Segments* numerous, linear, the largest 2.3–5.3 cm long and 3–7 mm wide, the margins entire. *Venation* reticulate. Nicaragua to Peru, West Indies; widespread in Costa Rica from 0 to 1,700 m, on the Caribbean and southwestern Pacific slopes.

Occasional trunk or bough epiphyte at La Selva, mainly in alluvial sites (Arboretum, pejiabay and *Citrus* groves).

*Polypodium pectinatum* and *P. hygrometricum* (among our species) are sometimes segregated into a separate subgenus (*Pectinatum*) or genus (*Pecluma* M. Price).

#### 16. *Polypodium sororium* Humb. & Bonpl. ex Willd.

*Rhizome* stout, short-creeping, densely covered with reddish-brown scales. *Petiole* 10–25 cm long. *Lamina* narrowly ovate, pinnate, 25–65 cm long, 7–25 cm wide, the basal pinnae mostly broadly attached. *Pinnae* 10–20 pairs, lanceolate, constricted at the base, marginally subentire, mostly 6–10 cm long and 8–22 mm

wide. *Venation* free. Southern Mexico to Venezuela, West Indies; widespread in Costa Rica, from 0 to 1,600 m.

Scattered throughout in primary forest understory; a low trunk epiphyte, usually on rather large trees.

#### 17. *Polypodium triseriale* Sw. (=*Goniophlebium triseriale* (Sw.) Pich-Serm.)

*Rhizome* stout, short- to long-creeping, covered with more or less spreading, dark brown scales. *Petiole* 12–36 cm long. *Lamina* ovate, fully pinnate, (15–)30–70 cm long and (12–)15–40 cm wide. *Pinnae* (2–)4–13 pairs, subsessile, lanceolate, the largest (8.5–)15–28 cm long and 1.7–4 cm wide, the margins entire. *Venation* reticulate. Southern Mexico to Bolivia, West Indies; widespread from 0 to 1,500 m in Costa Rica.

A canopy branch epiphyte, common at La Selva, both in alluvial and upland primary forest. Often encountered on downfalls, and seen low on trunks in the Arboretum, etc.

#### 28. PSEUDOCOLYSIS L. D. Gómez

EVANS, A. M. AND J. T. MICKEL. 1969. A re-evaluation of *Polypodium Bradeorum* and *P. colyoides*. *Brittonia* 21: 255–260.

GÓMEZ, L. D. 1977. Contribuciones a la pteridología centroamericana, II. *Novitates. Brenesia* 10/11: 115–119.

Epiphytes, the *rhizome* slender and long-creeping. *Fronds* essentially monomorphic, petiolate, the *lamina* simple or with a few lanceolate lobes. *Venation* reticulate. *Sori* linear, borne abaxially along the primary veins, exindusiate.

*Pseudocolysis* is closely related to *Polypodium* (s.l.), and the single species has generally been included within that genus; Stolze (1981) went so far as to tentatively assign it to subgenus *Pleopeltis*, with which it shares peltate laminar scales. But *Pseudocolysis* differs strikingly from all Central American *Polypodium* species in its linear sori, closely resembling some members of the Old World genus *Colyasis* in this respect (see Evans & Mickel, 1969). Tryon and Tryon (1982), while omitting *Pseudocolysis* from their formal classification, observed that it “certainly does not belong in any of the American genera of the Polypodiaceae (sensu stricto).” With these considerations in mind, we follow Gómez (1977) in treating this as a separate genus.

*Pseudocolysis* ranges from southern Mexico to Panama (Bocas del Toro).



1. **Pseudocolysis bradeorum** (Rosenstock) L. D. Gómez  
(=*Polypodium bradeorum* Rosenstock)

*Rhizome* rather slender, long-creeping, scaly. *Petiole* 5–20 cm long, somewhat scaly, winged toward the apex. *Lamina* simple and lanceolate to trilobate or pinnatifid and ovate, 8–18 cm long, scaly below, the margins subentire. *Segments* (when present) 1–3(–5) pairs, lanceolate, to ca. 9 cm long, 7–20 mm wide, narrowed at the base, acute apically. *Venation* reticulate. In Costa Rica, known only from below 200 m in the Caribbean lowlands (Llanuras de San Carlos and Sarapiquí).

A stem or branch epiphyte on understory treelets or shrubs, occasional to locally abundant at La Selva in secondary or primary alluvial forest (especially along rivers or quebradas, or in swamp forest); also on cacao.

Most La Selva material has simple to trilobate fronds. The unusual variation in leaf morphology exhibited by *Pseudocolysis bradeorum* prompted Tryon and Tryon (1982) to observe that this species “appears to have the attributes of a hybrid between widely different parents.” They nominated *Loxogramme mexicana* (Fée) C. Chr. (not known from below about 900 m in Costa Rica) and an unspecified species of *Polypodium* s.l. as the likeliest candidates.

## 29. PTERIS L.

SCAMMAN, E. 1961. The genus *Pteris* of Costa Rica. *Rhodora* 63: 194–205.

Terrestrial ferns, the *rhizome* erect or short-creeping. *Fronds* monomorphic, the *lamina* simply pinnate to (in ours) bipinnatifid or decom-pound, usually with the *basal pinnae* further elaborated. *Venation* free to reticulate. *Sori* linear and submarginal, covered by the recurved laminar margin.

A worldwide, largely tropical genus of 200–250 species, of which about 55 are neotropical. The latter range from central Mexico, south Florida and the Bahamas to southern Chile. About 14 indigenous species occur in Costa Rica. At La Selva, *Pteris* is likely to be confused only with *Lonchitis*, which differs most obviously in its copious pubescence.

### KEY TO THE SPECIES

1. Venation at least partly reticulate, with at least a single row of areolae along the costae of the penultimate segments.
2. Costa of penultimate segments with two or three

long areolae between the midribs of adjacent ultimate segments; penultimate segments not decurrent onto the rachis; laminar tissue membranaceous. . . . . 1. *P. altissima*.

2. Costa of penultimate segments with a single long areole between the midribs of adjacent ultimate segments; penultimate segments decurrent onto the rachis; laminar tissue somewhat chartaceous (papery). . . . . 2. *P. propinqua*.
1. Venation free.
  3. Pinnae 2–5 pairs, strongly reduced (except for the basal ones) at the base, the basal segments often mere nubs or auricles; some veins arising from the costa between adjacent segments; common. . . . . 3. *P. pungens*.
  3. Pinnae 5–15 pairs, slightly reduced basally, or not at all, the basal segments at least half as long as the longest ones; veins all arising from the midrib of the segment; very rare. . . . . 4. *P. quadriaurita*.

### 1. *Pteris altissima* Poiret

*Petiole* 40–135 cm long, smooth. *Lamina* del-tate to ovate, to 1.5 m long and 1.2 m wide. *Basal pinnae* greatly enlarged, bipinnate-pinnatifid, the apical portion pinnate-pinnatifid. *Penultimate segments* (pinnatifid pinnae) 25–35 cm long, 10–35 cm wide, caudate apically, the costae awned above at the junctions with costules. *Ultimate segments* lanceolate, acute to acuminate, the fertile ones 3–10 cm long, to 1.5 cm wide (sterile segments somewhat wider). Southern Mexico to Bolivia, West Indies; widespread in Costa Rica, from 0 to 2,200 m.

A large and coarse fern, rather uncommon at La Selva; it occurs only in low, wet areas in primary swamp forest and in primary to somewhat disturbed alluvial forest.

### 2. *Pteris propinqua* Agardh

*Petiole* 30–100 cm long. *Lamina* about as long, broadly ovate, mostly bipinnate-pinnatifid and often 2-forked basally, the *basal pinnae* much enlarged, the apical portion pinnate-pinnatifid. *Larger pinnae* to 37–42 cm long and 20–25 cm wide. *Ultimate segments* 11–20 pairs, falcate, 1.5–4 cm long and 5–10 mm wide. Southern Mexico to Bolivia, Jamaica; apparently restricted, in Costa Rica, to below 500 m on the Caribbean slope.

Rare at La Selva, known only from disturbed areas and at the edge of the forest on alluvial sites (e.g., Rafael's Point). A misidentified specimen of *Pteris propinqua* (Biolley 7491, CR) constitutes the basis for Scamman's (1961) erroneous report of *Pteris podophylla* Sw. from the La Selva vicinity (“confluence of Río Puerto Viejo and Sarapiquí”).

We follow A. R. Smith (pers. comm.) in rejecting the name *Pteris polita* Link for this entity.

### 3. *Pteris pungens* Willd.

*Petiole* 55–110 cm long. *Lamina* 23–60 cm long, 28–50 cm wide, somewhat pentagonal in outline, pinnate-pinnatifid. *Basal pinnae* bipartite, with some of the pinnules enlarged and themselves pinnatifid. *Penultimate segments* (pinnae) 2–5 pairs, 13–35 cm long, 2.5–8 cm wide, caudate apically, the costae awned above at junctions of costules. *Ultimate segments* to ca. 4–8 mm wide. Southern Mexico to Bolivia, West Indies; from 0 to 1,100 m in Costa Rica, on both slopes.

Widespread at La Selva in primary forest; this is our most common *Pteris* species.

### 4. *Pteris quadriaurita* Retz.

*Rhizome* stout, erect. *Petiole* to 36–100 cm long. *Lamina* 29–100 cm long and to ca. 50 cm wide, pinnate-pinnatifid, the *basal pinnae* bipartite with at least one pinnule enlarged and pinnatifid. *Pinnae* 5–15 pairs, the larger ones 14–36 cm long and 2–7.5 cm wide. *Ultimate segments* 1–3 cm long, 3–6 mm wide. Southern Mexico to Bolivia, West Indies; Africa, tropical Asia; widespread in Costa Rica from 0 to 1,800 m, on both slopes.

Although there are no recent collections of *Pteris quadriaurita* from La Selva, it is vouchered from the immediate vicinity (“confluence of Río Puerto Viejo and Sarapiquí”) by two old (and correctly identified) collections: *Biolley* 6933 and *Biolley* 7475 (CR). This species should be sought in disturbed or primary alluvial forest along the rivers.

## 30. SACCOLOMA Kaulf.

TRYON, R. 1962. Taxonomic fern notes. III. Contr. Gray Herb. 191: 91–107.

Terrestrial, the *rhizome* erect and scaly. *Fronds* monomorphic, the *lamina* simply pinnate to (in ours) decompound. *Venation* free. *Sori* marginal and pouch-like, covered on one side by a conical *indusium*.

A tropical genus of about 10 species, with 3 in the Americas and the remainder in Indomalaysia. The New World species range from southern Mexico and Cuba to southeastern Brazil, with two occurring in Costa Rica. *Saccoloma inaequale*, the species at La Selva, much resembles a small *Dennstaedtia*, but can be most easily dis-

tinguished from this closely related genus by its erect rhizome.

### 1. *Saccoloma inaequale* (Kunze) Mett.

*Petiole* half to about as long as lamina. *Lamina* deltate, generally 0.3–1 m long and 25–90 cm wide, 3–4-pinnate. *Basal pinnae* deltate, about 15–50 cm long and 8–35 cm wide. *Ultimate segments* mostly 1–2 cm long, crenate to lobed. Upper laminar surface generally somewhat convex above sori. Southern Mexico to Bolivia, West Indies; widespread in Costa Rica from 0 to 1,900 m. Plants at La Selva are considerably smaller, with smaller and differently textured laminae, than those from higher elevations.

One of the most common terrestrial ferns in primary forest at La Selva, generally occurring in or near natural disturbances or along trails.

## 31. SALPICHLAENA J. Smith

Terrestrial, the *rhizome* creeping (but the fronds approximate). *Fronds* slightly dimorphic. *Lamina* of young plants once-pinnate (the very youngest simple), the adult fronds bipinnate and prolonged indeterminately, twining high into trees (to 15 m, according to Tryon & Tryon, 1982). *Venation* free. *Sori* elongate, borne close to and parallel with the costa, indusiate.

This is one of our most distinctive ferns, unique in its tough, high-climbing fronds. Only in *Lycopodium* Sw., not known from La Selva, does an analogous growth habit occur. Nonetheless, the very close relationship of *Salpichlaena* to *Blechnum*, in which it is sometimes submerged, is plainly evident.

An ostensibly monotypic, neotropical genus, ranging from Nicaragua and the Lesser Antilles to Bahia.

### 1. *Salpichlaena volubilis* (Kaulf.) J. Smith (=*Blechnum volubile* Kaulf.)

*Lamina* chartaceous. *Pinnae* (of indeterminate fronds) 18–70 cm long, 18–60 cm wide. *Pinnules* 1–8 pairs (fewest on fertile fronds), on stalks 0.1–2.7 cm long, the sterile ones 9–14 cm long and 1.9–6 cm wide. *Fertile pinnules* 6–30 cm long and 0.7–2 cm wide. Widespread in Costa Rica from 0 to 1,600 m. Plants from higher elevations (1,000 m and above) in Costa Rica and Panama have much broader pinnules, and may not be conspecific.

Common throughout at La Selva, in primary forest and old secondary forest. The tenacious, high-twining rachises are a familiar and constant nuisance to bushwhackers.

32. **STIGMATOPTERIS** C. Chr.

CHRISTENSEN, C. 1909. On *Stigmatopteris*, a new genus of fern with a review of its species. Bot. Tidsskr. 29: 291-304.

———. 1913. A monograph of the genus *Dryopteris*. Part I. The tropical American pinnatifid-bipinnatifid species. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. Ser. 7, 10: 55-282.

Terrestrial ferns, the *rhizome* erect. *Fronde* monomorphic, the lamina once-pinnate to bipinnatifid, with microscopic, internal, pellucid glands. *Laminar* surfaces devoid of trichomes. *Venation* free (in ours), the veins ending before the margin in clavate hydathodes. *Sori* abaxial, round and exindusiate.

Our species of *Stigmatopteris* are difficult to distinguish in the field from *Thelypteris*, the best characters being the peculiar vein endings and pellucid laminar glands. Fortunately, both of the species at La Selva are quite rare, and not likely to be encountered.

A neotropical genus of 20-25 species, ranging from southern Mexico and Cuba to northeastern Argentina. The Costa Rican species number 6-7.

## KEY TO THE SPECIES

1. Pinnae crenately or serrately lobed, much less than halfway to the costa; pinnae in distal 1/2 to 1/3 of lamina with long-decurrent bases; basal pinnae less than 3 cm wide, the lowermost pairs separated by less than 5 cm on the rachis. . . . . 1. *S. longicaudata*.
1. Pinnae deeply pinnately lobed, to halfway or more to the costa; pinnae lacking long-decurrent bases, or such bases present only in the distal 1/4 or less of lamina; basal pinnae to more than 3 cm wide, the lowermost pairs separated by more than 5 cm on the rachis. . . . . 2. *S. sordida*.

1. ***Stigmatopteris longicaudata*** (Liebm.) C. Chr. (= *S. palmensis* Rosenstock)

*Petiole* 35-60 cm long, moderately scaly with dark brown scales. *Lamina* pinnate, terminating in a pinnatifid apex, broadly lanceolate, 45-75 cm long, the rachis moderately scaly. Free *pinnae* 10-20 pairs, the largest ones 15-25 cm long and 1.5-2.8 cm wide, crenate to serrate marginally. Southern Mexico to Venezuela and Bolivia; from 0 to 1,600 m on the Caribbean slope of Costa Rica.

Extremely rare at La Selva, and perhaps of ephemeral occurrence; known from a single, ster-

ile specimen collected along the Q. El Taconazo near the Sendero El Surá.

2. ***Stigmatopteris sordida*** (Maxon) C. Chr.

*Petiole* 20-65 cm long, bearing lax, broad, brownish scales, these rather remote except toward the base. *Lamina* pinnate-pinnatifid, terminating in a pinnatifid apex, broadly lanceolate to ovate, 35-85 cm long, the rachis remotely scaly. Free *pinnae* about 14-20 pairs, lobed about halfway to the costa or more, the largest ones 10-24 cm long and 3-3.5 cm wide. Mexico to Ecuador; restricted in Costa Rica to below 700 m on the Caribbean slope.

Very rare at La Selva, known by just a few collections from primary swamp forest (Plot II) and along sluggish portions of creeks (Q. Esquina). *S. sordida* is poorly known throughout its range.

33. **TECTARIA** Cav.

GRAYUM, M. H. 1987. On three misunderstood neotropical species of *Tectaria* (Polypodiaceae: Asplenioideae). Phytologia 64: 30-35.

MORTON, C. V. 1966. The Mexican species of *Tectaria*. Amer. Fern J. 56: 120-137.

Terrestrial ferns, the *rhizome* erect to creeping. *Petiole* not articulate with the rachis. *Fronde* essentially monomorphic, the *lamina* simple to pinnatifid, once-pinnate or decompound. *Venation* free (*T. brauniana*) or anastomosing. *Sori* (in ours) roundish, abaxial, indusiate or not.

A genus at once difficult to characterize, yet usually easily recognizable to the experienced eye. The petioles often have a reddish tinge, and the sori tend to be slightly irregular in distribution and sometimes also in shape, giving a patchy appearance. There is a tendency, in most species, for the basal pinnae to be more compound and elaborate than the others, often giving the lamina a deltate outline. The latter feature usually serves to distinguish similar species of *Tectaria* and *Thelypteris*. The terrestrial or epilithic habit and non-articulate petioles are sufficient to distinguish *Tectaria* from *Polypodium*.

A pantropical genus of 150-200 or more species, of which 35-40 are American. The latter range from south Texas, south Florida and Bermuda to northern Argentina. About 15 species occur in Costa Rica.

## KEY TO THE SPECIES

1. Lamina simple and entire, or palmately lobed.
  2. Lamina ovate, palmately lobed, rounded to cordate at base. . . . . 4. *T. heracleifolia*.
  2. Lamina oblong to oblanceolate, entire, attenuate at base. . . . . 8. *T. plantaginea*.
1. Lamina deeply pinnately lobed to pinnately compound.
  3. Venation free; lamina technically simple, the pinnae all connected by the pinnatifid wing of the rachis; pinnae again pinnately lobed; petiole and underside of rachis nearly black, pubescent; rare. . . . . 2. *T. brauniana*.
  3. Venation reticulate; lamina truly compound or, if not, the lobes entire; petiole and rachis reddish or, if darker, glabrous.
    4. Lamina simple, deeply pinnatifid.
      5. Rhizome stout, erect; lamina more than 50 cm long; rachis and major veins (below) glabrous; fresh crushed foliage with faint cyanide (burnt almond) odor. . . . . 3. *T. draconoptera*.
      5. Rhizome long-creeping; lamina mostly less than 50 cm long; rachis and major veins (below) densely puberulent; fresh crushed foliage lacking cyanide odor. . . . . 7. *T. nicotianifolia*.
    4. Lamina compound.
      6. Lamina pinnately compound, the pinnae entire to sinuately lobed (except basal pinnae usually with large, posterior basal lobe).
        7. Free pinnae usually 1–2 pairs; apical segment rounded to cordate at base; indusium circular, centrally attached. . . . . 4. *T. heracleifolia*.
        7. Free pinnae usually 4–10 pairs; apical segment usually decurrent on the rachis; indusium reniform, attached along the sinus. . . . . 5. *T. incisa*.
      6. Lamina bipinnately compound, the pinnae regularly and deeply lobed.
        8. Petiole, rachis and laminar surface abundantly and conspicuously soft villous-pubescent; lamina pinnate-pinnatifid, no pinnules truly free; stalks of lower pinnae less than 1.6 cm long; costal areolae with free included veinlets; indusium eciliate; very rare. . . . . 10. *T. rufovillosa*.
        8. Fronds not conspicuously pubescent to the naked eye; lamina pinnate-pinnatifid to subtripinnate, usually some with at least one pair of free pinnules; stalks of lower pinnae usually more than 1.6 cm long; costal areolae with or without free included veinlets; indusium ciliate or not.
          9. Very few areolae with free included veinlets (costal areolae always lacking them); petiole less than 50 cm long, light reddish-brown; indusium ciliate; common in disturbed habitats along rivers, etc. . . . . 6. *T. mexicana*.
          9. Many areolae with free included veinlets (costal areolae with or without them); petiole generally more than 50 cm long, medium brown to maroon; indusium ciliate or not.
            10. Areolae along costae, costules and distal part of rachis long, prominent, lacking free included veinlets; lamina pinnate-pinnatifid to subbipinnate (the basal pinnae simple, or with a single pair of free pinnules); 2–3 pairs of free pinnae below the pinnatifid apex; petiole longer than lamina, deep blackish-brown toward base, the scales few and restricted to the very base; indusia varying from linear to sublunate on the same frond, eciliate; primary swamp forest and along sluggish portions of quebradas. . . . . 1. *T. athyrioides*.
            10. Areolae along costae, costules and distal part of rachis with free included veinlets; lamina bipinnate to subtripinnate; generally 4–6 pairs of free pinnae below the pinnatifid apex; petiole about equaling lamina, dark reddish-brown to medium brown, conspicuously scaly in basal 10–20 cm; indusia regularly lunate, ciliate; primary riparian forest. . . . . 9. *T. rivalis*.

1. ***Tectaria athyrioides*** (Baker) C. Chr.  
(=*T. rheosora* (Baker) C. Chr.)

*Rhizome* very stout, short-creeping to sub-erect. *Petiole* of mature fronds (43–)56–95 cm long, this and the rachis deep chocolate-brown to maroon, blackish toward base where remotely and inconspicuously scaly. *Lamina* deltate, about (25–)39–67 cm long, simply pinnate-pinnatifid or the basal 1(–2) pairs of pinnae with a single pair of free pinnules. Free *pinnae* 2–3 pairs below the pinnatifid apex. *Basal pinnae* 18–40 cm long and about as wide, stalked by (1.7–)4.5–6.8 cm, the proximal pinnules broadly attached to stalked by 1–8(–18) mm. *Venation* reticulate, the costal areolae lacking free included veinlets. *Sori* irreg-

ular in shape and patchily distributed. *Indusia* linear to sublunate (on same lamina), evanescent, eciliate. Known definitely only from Nicaragua (Matagalpa, Zelaya) to Panama (Veraguas); from 0 to 1,100 m in Costa Rica, almost exclusively on the wetter parts of the Caribbean slope.

*Tectaria athyrioides* is of regular occurrence at La Selva in primary swamp forest and along sluggish sections of quebradas.

2. ***Tectaria brauniana*** (Karsten) C. Chr.  
(=*T. neotropica* L. D. Gómez)

*Rhizome* short- to long-creeping. *Petiole* 8–46 cm long, blackish, pubescent. *Lamina* broadly

lanceolate to deltate, 15–35 cm long and 9–29 cm wide, bipinnatifid (though not to the rachis), the basal pinnae larger and curving forward, with enlarged posterior basal pinnules that are themselves lobed. *Venation* free. Rachis and major veins pubescent below. Costae of lowermost pinnae diverging from the rachis at nearly a 90° angle. *Indusium* reniform. Costa Rica to Venezuela; from 50 to 900 m on the Caribbean slope of Costa Rica.

Occasional at La Selva in upland primary forest; it occurs only in especially wet places, such as seepages, where it may grow epilithically on rock faces.

3. ***Tectaria draconoptera*** (D. Eaton) Copel.  
(=*T. myriosora* (Christ) C. Chr.)

*Rhizome* stout, erect. *Petiole* stout, 30–110 cm long, scaly at base. *Lamina* pinnately lobed, the mature ones generally at least 50 cm long, somewhat longer than the petiole. Major *divisions* about 2–4 pairs, lanceolate to narrowly elliptic or oblanceolate, often more or less falcate, about 25–50 cm long and 7–13 cm wide, narrowed toward the base, acute to acuminate apically (sometimes forked), subentire, the basal pair often with a basal, posterior lobe. *Venation* copiously reticulate. *Indusium* lacking. Costa Rica to Peru; from below 600 m on the Caribbean coast of Costa Rica.

Occasional at La Selva in low areas in especially rich primary forest.

Various authors have expressed the suspicion (Stolze, 1981) or conviction (Tryon & Tryon, 1982) that *Tectaria draconoptera* and *T. nicotianifolia* are conspecific. Field observations at La Selva confirm that the differences noted in the key sharply delimit the two taxa.

4. ***Tectaria heracleifolia*** (Willd.) L. Underw.

*Rhizome* erect, the plants terrestrial, epilithic or (rarely) epiphytic. *Petiole* to 70 cm long (usually longer than lamina). *Lamina* simple and palmately lobed to trifoliolate or pinnate, deltate-ovate, to ca. 50 cm long and 25 cm wide. *Pinnae* (if any) 1–2 pairs, stalked, entire to sinuate, the basal ones the largest and usually with a strongly produced posterior lobe. *Apical segment* rounded to cordate at base. *Venation* reticulate. *Indusium* circular, peltate. Mexico to Peru, Florida, West Indies; widespread in Costa Rica from 0 to 1,500 m.

*Tectaria heracleifolia*, the most recent addition to the La Selva pteridophyte flora, is known from a single collection (Grayum 9445, CR), a simple-leaved individual growing at the base of a trunk along the Sendero Oriental at the Q. El Salto. This is, generally speaking, a common species,

and will no doubt turn up elsewhere on the property.

La Selva material belongs to var. *heracleifolia*, which shares the range of the species.

5. ***Tectaria incisa*** Cav.

*Rhizome* erect. *Petiole* 40–90 cm long. *Lamina* once-pinnate, oblong to ovate, 35–75 cm long and 20–65 cm wide. *Pinnae* 2–10 pairs, lanceolate to narrowly elliptic, mostly 20–30 cm long and 2.5–7 cm wide, subentire, the lower ones short-stalked. *Basal pinnae* with 1–2 large, posterior basal lobes. *Venation* reticulate. *Indusium* reniform to subcircular, somewhat persistent. Southern Mexico to Argentina, West Indies; widespread from 0 to 2,000 m in Costa Rica.

*Tectaria incisa* is frequent at La Selva along creeks and in secondary growth and old cacao, mostly on alluvial sites.

Occasional plants throughout the range of the species produce small buds or plantlets in the axils of the pinnae. These plants, which occur at La Selva, have received taxonomic recognition as forma *vivipara* (Jenman) C. Morton. The latter apparently corresponds to the recently described *Tectaria vivipara* Jermy & T. Walker.

6. ***Tectaria mexicana*** (Fée) C. Morton

*Rhizome* short-creeping to suberect. *Petiole* (12–)20–50 cm long, light reddish-brown to straw-colored. *Lamina* deltate, bipinnate- to tripinnate-pinnatifid in basal part, 20–50 cm long, (15–)30–50 cm wide. *Pinnae* 3–6 pairs, the basal pair 11–38 cm long, 5–30 cm wide, on stalks (0.9–)1.8–3.6 cm long, the basal posterior pinnules enlarged. *Venation* reticulate, with occasional free included veinlets. *Indusium* circular, persistent, the margin ciliate. Western and southern Mexico to Colombia; from 0 to 1,300 (to 2,400) m in Costa Rica.

Common at La Selva along rivers and larger quebradas, in secondary growth, etc., usually on alluvial sites. The more southern *Tectaria acutiloba* (Hieron.) Maxon appears to be vaguely, if at all, separated from this species.

7. ***Tectaria nicotianifolia*** (Baker) C. Chr.  
(=*T. euryloba* (Christ) Maxon)

*Rhizome* stout, long-creeping. *Petiole* 20–50 (–70) cm long, stout, abundantly scaly. *Lamina* ovate, pinnately lobed, 30–50(–60) cm long. Major *divisions* 2–4 pairs, lanceolate to elliptic or ovate, about 15–25 cm long and 4.5–8 cm wide (the terminal segment to 40 cm long and 15 cm wide), entire or broadly sinuate, acuminate to caudate apically, narrowed at the base. *Venation* copiously reticulate. *Indusium* lacking. Guate-

mala to Ecuador; from 0 to 900 m in Costa Rica, on both slopes.

Scattered throughout in primary forest or older secondary forest, often in low places or along creeks.

*Tectaria nicotianifolia* is related and superficially similar (especially when pressed and dried) to the much larger *T. draconoptera*.

#### 8. *Tectaria plantaginea* (Jacq.) Maxon

*Rhizome* creeping, the plants usually epilithic. *Petiole* 1.5–22 cm long, abundantly scaly. *Lamina* simple, oblong to oblanceolate, 10–41 cm long, 3.5–12 cm wide, obtuse apically (where occasionally viviparous), long-attenuate at base, the margins entire or weakly sinuate. *Venation* reticulate. *Indusium* lacking. Belize to Brazil, West Indies; from 0 to 800 m in Caribbean and south-western Costa Rica.

Terrestrial or more frequently epilithic; locally common at La Selva in and near rocky quebradas in upland primary forest.

Distinctive among our *Tectaria* species in its simple leaves, but might well be mistaken for a member of *Polypodium* subgenus *Campyloneurum*; the latter, however, are always epiphytic at La Selva.

#### 9. *Tectaria rivalis* (Mett. ex Kuhn) C. Chr.

*Rhizome* stout, short-creeping to suberect. *Petiole* about (40–)50–75 cm long, this and the rachis glossy reddish- or medium brown, darker toward base where conspicuously scaly. *Lamina* deltate, (40–)50–75 cm long, bipinnate to partly tripinnate in the basal part. Free *pinnae* generally 4–6 pairs below the pinnatifid apex. *Basal pinnae* by far the largest, (20–)40–50 cm long and (15–)40–45 cm wide, long-stalked (stalks 3.5–5.5 cm long), the free *pinnules* sessile to stalked (the stalks to about 1.7 cm long). *Venation* reticulate, with free included veinlets even in the costal areolae. *Indusium* lunate, soon deciduous, the margins ciliate. Belize to Colombia (Chocó); widespread from 0 to 1,000 (to 2,250) m in Costa Rica.

Locally common at La Selva in primary riparian forest along the R. Sarapiquí, as below the Sendero Ribereño and at the foot of Avenida Marañón; rare elsewhere, such as along the lower part of the Q. El Salto.

#### 10. *Tectaria rufovillosa* (Rosenstock) C. Chr.

*Rhizome* erect. *Petiole* 28–53 cm long, pubescent especially in apical part. *Lamina* deltate, pinnate-pinnatifid, 25–45 cm long and approximately as wide. Rachis, costae, veins and laminar tissue rusty-pubescent, especially below, the trichomes with yellowish-brown cross-walls.

*Pinnae* about 2–5 pairs below the pinnatifid apex, the lowermost deltate, 14–25 cm long and 11–23 cm wide, the basal, posterior lobes enlarged (to about 9–15 cm long) and themselves pinnatifid. Stalks of the basal pinnae 2–15 mm long. *Venation* reticulate, with free included veinlets (except in the costal areolae). *Indusium* circular to reniform, persistent, the margin eciliate. Nicaragua to Panama; distributed in Costa Rica from 100 m and below in the Caribbean lowlands, from the Llanuras de San Carlos south to the Río Sixaola region.

Very rare at La Selva, known from a single population along a low ridge in primary forest in the vicinity of CEN 160. *Tectaria rufovillosa* is a little-known and apparently rare fern throughout its range. *T. trinitensis* Maxon of Trinidad is nearly related and virtually indistinguishable from this species.

### 34. THELYPTERIS Schmidel

CHRISTENSEN, C. 1907. Revision of the American species of *Dryopteris* of the group of *D. opposita*. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. Ser. 7, 4: 247–336.

———. 1913. A monograph of the genus *Dryopteris*. Part I. The tropical American pinnatifid-bipinnatifid species. Kongel. Danske. Vidensk. Selsk. Skr., Naturvidensk. Afd. Ser. 7, 10: 53–289.

HOLTUM, R. E. 1969. Studies in the family Thelypteridaceae. The genera *Phegopteris*, *Pseudophegopteris*, and *Macrothelypteris*. Blumea 17: 5–32.

MAXON, W. R. AND C. V. MORTON. 1938. The American species of *Dryopteris*, subgenus *Meniscium*. Bull. Torrey Bot. Club 65: 347–376.

SMITH, A. R. 1971. Systematics of the neotropical species of *Thelypteris* section *Cyclosorus*. Univ. Calif. Publ. Bot. 59: 1–143.

———. 1980. Taxonomy of *Thelypteris* subgenus *Steiropteris*, including *Glaphyopteris* (Pteridophyta). Univ. Calif. Publ. Bot. 76: 1–38.

———. 1981. *Thelypteris* Schmidel. Pp. 473–514 in R. G. STOLZE, Ferns and fern allies of Guatemala. Part II. Fieldiana, Bot. n.s. 6: 1–522.

———. 1983. 14(4). Polypodiaceae—Thelypteridoideae. Pp. 1–147 in G. HARLING AND B. SPARRE, eds., Flora of Ecuador, No. 18. Univ. Göteborg, Stockholm.

Usually terrestrial plants, rarely epilithic (especially *T. francoana* at La Selva) or (elsewhere) even epiphytic. *Rhizome* erect to short- or long-creeping. *Fronde* monomorphic to slightly dimorphic, with at least some simple to forked or stellate trichomes. *Lamina* most typically pinnate-pinnatifid, but ranging in our species from simple and entire to decompound. *Venation* free to reticulate. *Sori* abaxial, round to elliptical, ex-indusiate or with a reniform indusium.

At La Selva, any terrestrial fern with regularly pinnate to pinnate-pinnatifid laminae, fewer than 40 pinnae and round, abaxial sori is likely to

belong to this genus; only *Stigmatopteris* cannot be separated by these characters, but our species are extremely rare. Anomalous species of *Thelypteris* must be learned individually. *T. francoana* and *T. gigantea* are easily recognized as members of their respective subgenera (*Goniopteris* and *Meniscium*), even though their laminae have been reduced to a single pinna. Care must be taken, however, to distinguish the decomposed-leaved *Thelypteris torresiana* from species of *Ctenitis* and *Lastreopsis*.

*Thelypteris* has often been divided into numerous smaller genera, especially by Old World authors; however, recent New World authorities

have tended to maintain the genus in the broadest sense, as treated here. Several of the taxa accorded the rank of subgenus in this treatment are rather distinctive and easily learned, especially *Meniscium* and *Goniopteris*. The La Selvan species of *Thelypteris* are here keyed artificially, but grouped by subgenus in the text.

A huge, cosmopolitan genus of 900–1,000 species, largely tropical but also represented in temperate regions. The 325–350 New World species range from Alaska to Chile and Argentina. About 94 species are known from Costa Rica. *Thelypteris* is the largest genus of pteridophytes at La Selva.

#### KEY TO THE SPECIES

1. Leaves simple.
  2. Margins crenately lobed, the lamina less than 3 cm wide. . . . . 8. *T. francoana*.
  2. Margins entire, the lamina more than 3 cm wide. . . . . 16. *T. gigantea*.
1. Leaves compound, pinnate to bipinnate-pinnatifid.
  3. Leaves bipinnate-pinnatifid; petiole glaucous at base. . . . . 13. *T. torresiana*.
  3. Leaves pinnate to pinnate-pinnatifid, sometimes deeply so, but then the lobes entire; base of petiole not glaucous.
    4. Basal pinnae greatly reduced, ultimately to less than 1 cm in length and less than  $\frac{1}{10}$  as long as the longest pinnae.
      5. Pinna margins pinnately lobed halfway or more to the costa; pinnae lacking basal, anterior lobe; laminar surface with minute, reddish glands below.
        6. Longest pinnae more than 3 cm long, abruptly reduced below; lobes usually perpendicular to the costa, each with more than 10 pairs of nerves; petiole more than 5 cm long; common. . . . . 1. *T. balbisii*.
        6. Longest pinnae less than 3 cm long, gradually reduced to the base of the frond; lobes spreading obliquely to the costa, each with fewer than 10 pairs of nerves; petiole very short, less than 5 cm long; very rare. . . . . 2. *T. resinifera*.
      5. Pinna margins subentire to crenate or serrate, less than halfway to the costa; pinnae with prominent basal, anterior lobe; laminar surface below lacking minute, reddish glands; very rare. . . . . 3. *T. villana*.
    4. Basal pinnae not reduced, or not so greatly.
      7. Pinna margins entire to shallowly crenate or uncinately serrate, the rachis and laminar surface never pilose; sori often confluent at maturity.
        8. Pinna margins entire to obscurely crenulate.
          9. Pinnae usually 6 or more pairs, less than 4 cm wide.
            10. Lower pinnae less than 18 cm long, sessile or with stalks less than 8 mm long; plants smaller; common along rivers, etc. . . . . 14. *T. angustifolia*.
            10. Lower pinnae usually over 18 cm long, with conspicuous stalks at least 8 mm long; plants large, the fronds often over 1 m long; rare. . . . . 15. *T. falcata*.
          9. Pinnae usually fewer than 6 pairs, more than 4 cm wide. . . . . 17. *T. lingulata*.
        8. Pinna margins serrate to uncinately serrate. . . . . 18. *T. serrata*.
      7. Pinna margins shallowly to very deeply crenately lobed or, if subentire, the laminar surface and rachis pilose; sori discrete.
        11. Fronds variously pubescent, but the trichomes never forked or stellate; laminar surface usually pubescent above, at least toward the margin.
          12. Pinnae less than 7 pairs, shallowly crenately lobed (to much less than halfway to the costa); rhizome long-creeping, the fronds arising distantly. . . . . 9. *T. ghisbreghtii*.
          12. Pinnae more than 7 pairs, deeply lobed (to at least halfway to the costa); rhizome erect to short-creeping, the fronds approximate.
            13. Aerophores (small peglike outgrowths or dark glandular bodies) subtending each costa along the underside of the rachis; fronds often pendent.
              14. Plants large, the fronds more than 1 m long; laminar surface pubescent above; pinnae lobed about  $\frac{2}{3}$  the way to the costa; sori lacking indusia. . . . . 19. *T. decussata*.
              14. Plants small, the fronds less than 1 m long; laminar surface glabrous above;

- pinnae lobed about  $\frac{1}{2}$ – $\frac{3}{4}$  the way to the costa; sori with pubescent indusia. . . . . 20. *T. leprieurii*.
13. Aerophores absent; fronds usually erect or arching.
15. Trichomes on underside of costa uniform, less than 0.1 mm long; petioles usually reddened; rhizome short-creeping. . . . . 4. *T. dentata*.
15. Trichomes on underside of costa of various lengths, some more than 0.5 mm long; petioles greenish or straw-colored; rhizome erect. . . . . 5. *T. hispidula*.
11. Fronds with stellate or bifid trichomes, at least along the rachis (these may be appressed and difficult to see).
16. Rhizome long-creeping, the fronds arising separately; pinnae shallowly lobed, 3–4 pairs of veins uniting below each sinus. . . . . 11. *T. poiteana*.
16. Rhizome erect, the fronds approximate; pinnae shallowly lobed, 0–2 pairs of veins uniting below each sinus.
17. Rachis densely and conspicuously pubescent with dark brown hairs; laminar surface abundantly appressed-pubescent above. . . . . 7. *T. curta*.
17. Pubescence of rachis minute, inconspicuous; laminar surface glabrous above, or slightly pubescent toward the margins.
18. Pinnae lobed at least halfway to the costa, or, if not, the terminal pinna conform (similar to the lateral pinnae).
19. Petiole grooved above nearly to the summit; rachis bearing minute trichomes which are forked apically, with the arms short and recurved; apical segment pinnatifid; rare. . . . . 6. *T. biolleyi*.
19. Petiole grooved above only in the basal half; rachis without anchor-shaped trichomes; terminal pinna conform; very common. . . . . 10. *T. nicaraguensis*.
18. Pinnae lobed less than halfway to the costa; terminal segment pinnatifid, hastately lobed; rare. . . . . 12. *T. urbanii*.

#### Subgenus AMAUROPelta

1. ***Thelypteris balbisii*** (Sprengel) Ching  
(=*T. mercurii* (A. Braun ex Hieron.) C. Reed)

*Rhizome* erect, the fronds clustered. *Petiole* 5–28 cm long, much shorter than the lamina, scaly toward the base. *Lamina* membranaceous, lanceolate, 45–110 cm long, pinnate-pinnatifid, with reddish glandular dots below. *Pinnae* numerous, sessile, subopposite, lanceolate, mostly 5–20 cm long and 1–3 cm wide, deeply lobed, the basal 8–10 pairs much reduced and widely spaced. *Rachis* more or less hairy, with brownish peg-like aerophores subtending the costae. *Sori* with small, tan indusia. Southern Mexico to Venezuela and Ecuador, West Indies; widespread in Costa Rica from 0 to 1,300 m.

*Thelypteris balbisii* is very common at La Selva along the rivers and major quebradas.

2. ***Thelypteris resinifera*** (Desv.) Proctor  
(=*T. pseudosantha* (C. Chr.) C. Reed; *Amauropelta resinifera* (Desv.) Pichi-Serm.)

*Rhizome* erect. *Petiole* 1–8 cm long, much shorter than the lamina. *Lamina* lanceolate, 15–100 cm long, 3–30 cm wide, pinnate-pinnatifid with a pinnatifid apex, membranaceous, with reddish glands below. *Pinnae* 22–40 pairs, opposite or alternate, narrowly lanceolate, 1–16 cm long and 3–16 mm wide (with several basal pairs much reduced), deeply lobed. *Sori* with roundish indusia. Mexico to Ecuador, Florida, West In-

dies; widespread in Costa Rica, from 0 to 1,700 m.

*Thelypteris resinifera* is extremely rare at La Selva, or perhaps it has been overlooked; it is known from just two collections, both from along the banks of the R. Puerto Viejo.

La Selva specimens of *Thelypteris resinifera* occupy the low end of the range for most measurements given above and, in this respect, agree well with the description of *T. pseudosantha*. Plants of *T. resinifera* occur in the same habitat at La Selva as our most abundant member of subgenus *Amauropelta*, *Thelypteris balbisii*, and might easily be mistaken for juveniles of that species.

3. ***Thelypteris villana*** L. D. Gómez  
(=*T. pseudoaspidioides* L. D. Gómez)

Plants generally epilithic, the *rhizome* stout, erect, to about 8 cm long. *Petiole* 1–13 cm long. *Lamina* lanceolate to narrowly elliptic, 7–25 cm long and 2–6 cm wide, once-pinnate with a pinnatifid apex. Free *pinnae* 7–16 pairs, subopposite to alternate, the larger ones 1.1–3.6 cm long (the lower ones much reduced), the margins entire to crenate or serrate, with a prominent basal anterior lobe. *Sori* round to slightly elongate, ex-indusiate, in a single row on either side of the costa. Costa Rica and Panama; from 50 to 1400 m on the Caribbean slope of Costa Rica.

Known from the vicinity of La Selva only by *Chacón 1233* (CR), growing “en paredones del Río Peje,” near the Cloud Forest Ridge. It has



yet to be collected from La Selva proper, but should be sought along rocky quebradas in the southern portion of the property.

*Thelypteris villana*, comprising smallish plants with simply pinnate laminae, does not resemble any of our other species of the genus. Although originally described as a member of subgenus *Goniopteris*, it is identical to the more recent *T. pseudoaspidioides*, which was properly assigned to subgenus *Amauropelta*.

#### Subgenus CYCLOSORUS

4. ***Thelypteris dentata*** (Forsskal) St. John  
(=*Cyclosorus dentatus* (Forsskal) Ching;  
*Christella dentata* (Forsskal) Brownsey &  
Jermy)

*Rhizome* short-creeping. *Fronde*s slightly dimorphic, the fertile ones taller and with more numerous, narrower pinnae. *Petiole* 15–45 cm long, reddish or purplish, scaly toward base. *Lamina* lanceolate, pinnate-pinnatifid with a pinnatifid apex, 30–90 cm long and 14–34 cm wide, pubescent below. *Pinnae* numerous, mostly 6–17 cm long and 1.1–2.7 cm wide, lobed more than halfway to the costa, the lowermost 2–6 pairs reduced. *Sori* with pubescent indusia. Native in Africa, Asia and Oceania; widely naturalized in the New World from southern Mexico to Argentina, and in the southeastern United States and the West Indies; widespread in Costa Rica from 0 to 1,200 m.

A common, weedy species at La Selva in open habitats, such as the pejibaye grove and the Successional Strips. It is occasionally seen in well-lit sites in upland primary forest, such as along quebradas.

In the field, *Thelypteris dentata* is scarcely to be distinguished from *T. hispidula*, which occurs in the same habitats. These two species are unique among La Selva *Thelypteris* in having a black, rather than brown, spore print.

5. ***Thelypteris hispidula*** (Decne.) C. Reed  
(=*T. quadrangularis* (Fée) Schelpe; *Cyclosorus quadrangularis* (Fée) Tard.; *Christella hispidula* (Decne.) Holttum)

*Rhizome* suberect to erect. *Petiole* mostly straw-colored, 10–50 cm long, pubescent. *Lamina* lanceolate, 18–70 cm long and 8–30 cm wide, pinnate-pinnatifid with a pinnatifid apex, pubescent below. *Pinnae* numerous, sessile, mostly 4–15 cm long and 0.8–2.5 cm wide, lobed more than halfway to the costa, the lowermost 2–4 pairs reduced. *Sori* with pubescent indusia. Pantropical in distribution but, unlike *Thelypteris dentata*, believed to be native throughout its range;

occurring in the New World from Mexico to Bolivia, and in the West Indies; from 0 to 900 m on both coasts of Costa Rica.

Occasional at La Selva in weedy areas, secondary growth and abandoned cacao.

*Thelypteris hispidula* occurs in the same habitats as the very similar *T. dentata*, our only other member of subgenus *Cyclosorus*, from which it may be distinguished in the field by its erect rhizome and pale-colored petioles.

#### Subgenus GONIOPTERIS

6. ***Thelypteris biolleyi*** (Christ) Proctor  
(=*Goniopteris biolleyi* (Christ) Pichi-Serm.)

*Rhizome* erect. *Petiole* 30–75 cm long, brownish, sulcate adaxially nearly to base of lamina. *Lamina* broadly lanceolate, 45–80 cm long and 15–45 cm wide, pinnate-pinnatifid with a pinnatifid apex. *Pinnae* 16–22 pairs, sessile or short-stalked, lanceolate, 7–22 cm long and 2–3.5 cm wide, lobed about halfway to the costa. *Sori* exindusiate. Southern Mexico to Peru, Jamaica; apparently restricted in Costa Rica to below 700 m in the Caribbean lowlands.

Known at La Selva only from secondary growth and abandoned cacao groves on recent alluvium.

Although rare at La Selva, *Thelypteris biolleyi* occurs in much-frequented areas and is thus likely to be encountered. It grows alongside and closely resembles the nearly related and much more abundant *T. nicaraguensis*, from which it may be distinguished in the field by its larger size and extensively grooved petioles. The microscopic, anchor-shaped hairs are diagnostic.

7. ***Thelypteris curta*** (Christ) C. Reed

*Rhizome* erect. *Petiole* to 50 cm long. *Lamina* lanceolate in outline, pinnate-pinnatifid with a pinnatifid apex, 20–40 cm long and 11–28 cm wide, appressed-pubescent above. *Pinnae* numerous, attenuate, sessile or the lowermost short-stalked, lanceolate, 6–14 cm long and 1.5–2.5 cm wide, lobed halfway or more to the costa. *Rachis* densely brownish-tomentose. *Sori* with reddish-brown, setose indusia. Costa Rica to Ecuador; from 0 to 1,500 m in Caribbean and southwestern Costa Rica.

Locally common at La Selva in primary alluvial forest, especially on slopes or banks near quebradas.

The narrow laminae and brownish-tomentose rachis distinguish *T. curta* from all of our other *Thelypteris* species. This is the only La Selvan species in subgenus *Goniopteris* (and one of our few species of *Thelypteris*) that occurs characteristically in undisturbed primary forest.

8. ***Thelypteris francoana*** (Fourn.) C. Reed  
(=*Goniopteris francoana* (Fourn.) A. Löve & D. Löve)

*Rhizome* suberect, sometimes briefly prolonged. *Fronds* clustered at the summit, often arching outward and pointing down. *Petiole* 2.5–20 cm long, usually shorter than the lamina. *Lamina* simple, narrowly lanceolate, 5.5–25 cm long and 0.7–2.5 cm wide, pinnately lobed less than halfway to the midrib, cuneate at the base, somewhat chartaceous. *Sori* with small, setose-margined indusia. Nicaragua to Ecuador; from 0 to 800 m in Costa Rica, mainly on the Caribbean slope (very rare on the Pacific slope).

*Thelypteris francoana* is a true rheophyte, being restricted to more or less steep muddy or rocky banks of the rivers and major quebradas at La Selva, where it is usually conspicuous due to the narrow, pendent laminae. The plants are frequently epilithic.

*Thelypteris francoana* is our only simple-leaved member of subgenus *Goniopteris*; its relationship to the other, more typical members of this group is nonetheless obvious, even superficially.

9. ***Thelypteris ghiesbreghtii*** (Hook.) C. Morton  
(=*Goniopteris mollis* Fée)

*Rhizome* long-creeping, the fronds solitary or distant. *Petiole* 30–85 cm long. *Lamina* ovate, 16–55 cm long and 15–40 cm wide, once-pinnate with a conform terminal pinna, densely pilose beneath with simple trichomes. *Pinnae* 2–5 pairs, sessile, elliptic, 10–30 cm long and 3.5–8 cm wide, the margins entire to irregularly serrulate or lobed. *Sori* exindusiate or essentially so. Chiapas to Panama; from 0 to 1,300 m in Costa Rica, most common on the Caribbean slope.

Uncommon at La Selva, in secondary forest and abandoned cacao groves on recent alluvium.

An aberrant (in lacking branched trichomes) member of subgenus *Goniopteris*, *Thelypteris ghiesbreghtii* is easily recognized by its solitary, softly pubescent fronds with few, broad pinnae.

10. ***Thelypteris nicaraguensis*** (Fourn.) C. Morton

*Rhizome* short-creeping. *Petiole* 25–60 cm long. *Lamina* ovate, 25–50 cm long and 25–40 cm wide, pinnate-pinnatifid with a conform terminal pinna. *Pinnae* 7–12 pairs, 12–22 cm long and 2–5 cm wide, lobed about halfway to the costa. *Sori* exindusiate. Southern Mexico to Panama; from 0 to 900 m in Costa Rica, on both slopes.

Common at La Selva in open, weedy areas, trailsides, secondary growth and abandoned cacao groves; it also occurs sparingly in upland

primary forest, in well-lit situations such as along quebradas.

*T. nicaraguensis* is our most abundant and conspicuous *Thelypteris* species in habitats most frequented by humans. Though normally terrestrial, it is quite versatile and has been collected on rocks or logs, and even as a low trunk epiphyte.

Collections from La Selva have often been misdetermined as *T. tristis* (Kunze) C. Morton; according to A. R. Smith (1983; pers. comm.), that species does not occur north of Panama.

11. ***Thelypteris poiteana*** (Bory) Proctor  
(=*Goniopteris poiteana* (Bory) Ching)

*Rhizome* short- to long-creeping, the fronds solitary or few, slightly dimorphic (the fertile ones with longer stipes). *Petiole* 15–45 cm long, glabrescent. *Lamina* ovate, 20–40 cm long, 17–30 cm wide, once-pinnate with a conform terminal pinna. *Pinnae* 2–6 pairs, narrowly elliptic to lanceolate, sessile or short-stalked, 8–22 cm long and 3–6 cm wide, the margins entire to serrate or shallowly lobed. *Sori* exindusiate. Southern Mexico to Ecuador and northern Brazil, West Indies; from 0 to 700 m on the Caribbean coast of Costa Rica, and on the Pacific slope of the Cordillera de Guanacaste.

Uncommon at La Selva in open, weedy areas, as the Arboretum and the pejobaye grove.

*Thelypteris poiteana* has the same growth habit as *T. ghiesbreghtii*, to which it is believed closely related, but the fronds more resemble those of *T. nicaraguensis*.

12. ***Thelypteris urbanii*** (Sodi) A. R. Smith  
(=*T. leucophlebia* (Christ) C. Reed; *Goniopteris leucophlebia* (Christ) Ching)

*Rhizome* suberect. *Petiole* 30–100 cm long. *Lamina* deltate to ovate, 35–100 cm long and 30–60 cm wide, pinnate-pinnatifid, the terminal segment confluent and usually hastate. *Pinnae* lanceolate, 20–30 cm long and 3.5–4.5 cm wide, lobed less than halfway to the costa. *Sori* very small, with minute indusia. Nicaragua to Ecuador; from 0 to 200 (to 1,200) m in Costa Rica, on the Caribbean slope and the Osa Peninsula.

This species is rather rare at La Selva and, apparently, throughout its range. Our few collections are from slopes in old secondary or disturbed primary forest on recent alluvium, as along the trail into Plot I.

*Thelypteris urbanii* is quite nondescript, but may be distinguished from other species of subgenus *Goniopteris* at La Selva by its shallowly lobed pinnae and hastate terminal segment.

N.B.: *Thelypteris* (*Goniopteris*) *eggersii* (Hieron.) C. Reed has been collected from along the R. Peje, just off the property (*Chacón 1241*, MO). This species would key roughly to *T. biolleyi* in the present treatment, but differs from the latter in its glabrous lower leaf surfaces and setose indusia.

#### Subgenus MACROTHELPTERIS

13. *Thelypteris torresiana* (Gaudich.) Alston  
(=*Macrothelypteris torresiana* (Gaudich.) Ching)

*Rhizome* short-creeping to suberect. *Petiole* 20–70 cm long, scaly and glaucous toward the base. *Lamina* ovate, 28–100 cm long and 18–60 cm wide, bipinnate-pinnatifid, membranaceous, the axes and veins below with whitish trichomes. *Pinnae* deltate to lanceolate, the largest ones 10–34 cm long and 3.5–16 cm wide, pinnate (but with the costa narrowly winged). *Sori* with minute indusium. Native in tropical and subtropical Africa, Asia and Oceania; widely established in the Western Hemisphere from southern Mexico to northern Argentina, and in the southeastern United States and the West Indies; widespread in Costa Rica from 0 to 2,100 m.

Occasional at La Selva, mostly in disturbed areas on recent alluvium: along the rivers and lower portions of the major quebradas, and in secondary growth and abandoned cacao groves. It is occasionally seen in light gaps in upland primary forest.

The decomposed laminae at once set *T. torresiana* apart from every other New World *Thelypteris*; at La Selva, it is more apt to be mistaken for a *Ctenitis* or *Lastreopsis*, from which it may be distinguished in the field by the whitish-pubescent foliage and glaucous petioles.

#### Subgenus MENISCIUM

14. *Thelypteris angustifolia* (Willd.) Proctor  
(=*Meniscium angustifolium* Willd.)

*Rhizome* short-creeping. *Petiole* 10–50 cm long, longer on fertile than on sterile fronds. *Lamina* ovate to lanceolate in outline, 15–50 cm long, once pinnate with a conform terminal pinna. *Pinnae* 6–20 pairs, lance-linear, 5–18 cm long and 1–2 cm wide, subentire, attenuate at apex, sessile or the lower ones stalked to about 8 mm. *Sori* becoming confluent. Mexico to Paraguay, West Indies; from 0 to 1,100 m in Costa Rica, on both slopes.

Common at La Selva on rocky banks of rivers and major quebradas.

Typical *Thelypteris angustifolia*, with lanceolate laminae and more than 10 pairs of pinnae

(e.g., *Grayum 2115*), is less common at La Selva than a form with ovate laminae and fewer than 10 pairs of pinnae (*Grayum 1236, 2065*). These latter plants may belong to a different species but, if so, it is apparently an undescribed one.

15. *Thelypteris falcata* (Liebm.) R. Tryon  
(=*Meniscium falcatum* Liebm.)

*Rhizome* short-creeping. *Petiole* ca. 50–100 cm long. *Lamina* broadly lanceolate, ca. 50–100 cm long and 25–70 cm wide, once-pinnate with a conform terminal pinna. *Pinnae* 8–20 pairs, somewhat curved, the lower ones long-stalked (8–16 mm), 15–35 cm long and 1.8–4 cm wide, widest near the middle, the margins entire or subentire. *Sori* exindusiate. Oaxaca to Bolivia, Cuba; from 0 to 1,200 m in Caribbean and southwestern Costa Rica.

Quite rare at La Selva, where it is widely scattered in old secondary forest and upland primary forest.

*Thelypteris falcata* is similar in aspect to *T. angustifolia*, but generally much larger. The plants bear a strong superficial resemblance to *Metaxya rostrata*.

16. *Thelypteris gigantea* (Mett.) R. Tryon  
(=*Meniscium giganteum* Mett.)

*Rhizome* suberect. *Fronde*s slightly dimorphic, the fertile ones smaller and on longer petioles. *Petioles* 9–60 cm long, brownish. *Fertile lamina* simple, narrowly elliptic to lanceolate, 35–70 cm long and 7–15 cm wide, cuneate at the base, the margins entire to crenulate. *Sori* exindusiate. Costa Rica to Peru; from 50 to 1,500 m on the wetter parts of the Caribbean slope of Costa Rica.

Rare at La Selva, known only from low, poorly drained areas and along small quebradas in upland primary forest toward the southern end of the property.

*Thelypteris gigantea* is our only simple-leaved member of subgenus *Meniscium*; it is quite similar in all other respects to more typical members of that taxon, such as *T. lingulata*. Though a fair-sized and rather striking fern, there is nothing particularly “gigantic” about this species (unless one considers that the lamina actually corresponds to a single pinna).

17. *Thelypteris lingulata* (C. Chr.) C. Morton

*Rhizome* short-creeping or suberect. *Petiole* about 60–100 cm long. *Lamina* ovate, 45–60 cm long, once-pinnate with a conform terminal pinna. *Pinnae* 3–5 pairs, widely spaced, 15–35 cm long and 4.5–8 cm wide, the lower ones sessile or (more usually) stalked (1–3 cm). *Sori* exin-

dusiate, paired, becoming confluent. Nicaragua to Peru; from 0 to 500 m on the Caribbean slope of Costa Rica.

A common and conspicuous fern at La Selva, widespread in the primary forest understory.

18. *Thelypteris serrata* (Cav.) Alston  
(=*Meniscium serratum* Cav.)

*Rhizome* short-creeping. *Petiole* to at least 55 cm long, glabrate. *Lamina* lanceolate, 45–90 cm long and 14–45 cm wide, once-pinnate with a conform terminal pinna. *Pinnae* 15–25 pairs, narrowly lanceolate, the lower ones short-stalked, 8–25 cm long and 1.5–4.5 cm wide, the margins serrate (with the teeth often hooked). *Sori* ex-indusiate. Southern Mexico to Argentina, Florida, West Indies; from 0 to 1,200 m in Costa Rica, on both slopes.

Although common in adjacent parts of Costa Rica, *Thelypteris serrata* is rather rare at La Selva; it occurs principally in open, wet areas, such as along the rivers and major quebradas and in *Spathiphyllum* marshes. One collection is from a small quebrada (Q. Esquina) in upland primary forest.

This is our only species in subgenus *Meniscium* with serrate pinna margins.

Subgenus STEIROPTERIS

19. *Thelypteris decussata* (L.) Proctor  
(=*Glaphyopteris decussata* (L.) Fée)

*Rhizome* stout, erect, covered apically with gelatinous slime. *Fronde* erect, or arching downward if the plants are growing on a declivity. *Petioles* scaly at base, to 1.2 m long. *Lamina* broadly lanceolate, 1–2.3 m long and 30–90 cm wide, pinnate-pinnatifid with a pinnatifid apex, pubescent above. *Pinnae* numerous, narrowly lanceolate, the larger ones 15–45 cm long and 2.5–4.5 cm wide, sessile, deeply lobed into narrow segments. *Costae* subtended abaxially by stout *aerophores* to 10 mm long. *Sori* tiny, ex-indusiate. Guatemala to Peru and southern Brazil, West Indies; mostly in Caribbean and southwestern Costa Rica, from 0 to 1,700 m.

Though abundant in adjacent areas, *Thelypteris decussata* is rather uncommon at La Selva; the plants are widely scattered, mostly near creeks and in disturbed areas in upland forest.

*Thelypteris decussata* var. *costaricensis* A. R. Smith, endemic to Costa Rica, occurs at La Selva.

20. *Thelypteris leprieurii* (Hook.) R. Tryon

*Rhizome* short-creeping. *Fronde* 60–140 cm long, often arching outward and hanging down.

*Lamina* 30–70 cm long, lanceolate, pinnate-pinnatifid with a pinnatifid apex, glabrous above. *Pinnae* 5–17 cm long, lobed more than halfway to the costa. *Aerophores* at base of pinnae prominent, about 1–2 mm long. *Sori* with pubescent indusium. Costa Rica to Bolivia and southeastern Brazil; from 50 to 2,000 m on the wetter parts of the Caribbean slope in Costa Rica.

This species has been collected in the immediate vicinity of La Selva just twice, from steep banks along the R. Peje, just off the southwestern boundary. It is abundant in the Chilamate area, but is not yet known from La Selva proper.

The Costa Rican representative of *Thelypteris leprieurii* is var. *subcostalis* A. R. Smith, which ranges from Costa Rica to Colombia.

35. VITTARIA J. E. Smith

BENEDICT, R. C. 1914. A revision of the genus *Vittaria* J. E. Smith. Bull. Torrey Bot. Club 41: 391–410.

Small to medium-sized epiphytic ferns, the *rhizome* short-creeping to suberect. *Roots* with felt-like hairs. *Petiole* absent or brief. *Fronde* monomorphic, the lamina simple, glabrous, narrowly linear to linear-lanceolate, the margins entire to remotely and irregularly 1–few-toothed or -lobed. *Venation* reticulate, without free included veinlets. *Sori* submarginal or nearly marginal, continuous, lacking indusia.

A pantropical genus of 50–75 species, about 12 of which occur in the New World from the southeastern United States to Argentina and Uruguay. About 9 species are known for Costa Rica.

KEY TO THE SPECIES

1. Areolae in 2–several rows on each side of the midvein; largest sterile laminae more than 1 cm wide; at least some of the laminae usually with a blunt tooth or lobe. . . . . 1. *V. costata*.
1. Areolae in a single row on each side of the midvein; largest laminae rarely if ever more than 1 cm wide, always entire.
  2. Lamina narrowly linear, grasslike, the largest less than 3.5 mm wide, without a definite, terete petiole. . . . . 2. *V. lineata*.
  2. Lamina broader, the largest more than 3.5 mm wide, with a brownish, terete petiole more than 1 cm long. . . . . 3. *V. stipitata*.
1. *Vittaria costata* Kunze  
(=*Ananthacorus angustifolius* (Sw.) L. Underw. & Maxon)

*Rhizome* short-creeping, with abundant, grayish-brown, iridescent scales toward apex. *Fronde*

pendent, the *petioles* obsolete. *Lamina* linear or narrowly oblanceolate, 12–55 cm long, 4–18 mm wide, the margins entire or occasionally with a single, low, blunt tooth or lobe. *Areolae* in several rows on each side of the midvein. Mexico to Surinam and Bolivia, West Indies; common in Costa Rica from 0 to 1,300 m on both slopes.

Occasional trunk or branch epiphyte in secondary and primary forest throughout; frequent on cacao.

## 2. *Vittaria lineata* (L.) J. E. Smith

*Rhizome* short-creeping, with reddish to grayish scales, these tapering to an elongate, filiform apex. *Fronde*s arching or pendent, the *petiole* obsolete. *Lamina* narrowly linear, thickish, (5–)25–100 cm long and 1–3 mm wide, the margins entire. *Areolae* in a single row on each side of the midvein. Mexico to Paraguay, southeastern United States, West Indies; from 0 to 2,000 m in Costa Rica (though most common below about 500 m), on both slopes.

Common and widespread at La Selva, mostly as a canopy epiphyte but descending along rivers and other well-lit habitats (pejibaye grove).

Mature plants of *Vittaria lineata* are remarkably grasslike and very distinctive; however juvenile plants, which may be precociously fertile, have much shorter and relatively broader laminae and superficially resemble mature specimens of *Grammitis linearifolia*. They may be distinguished from the latter species by their marginal, rather than medial, sori.

## 3. *Vittaria stipitata* Kunze

*Rhizome* suberect, with dark brown, filiform scales. *Fronde*s rather limply pendent, the *petiole* 1–5 cm long, terete and dark brownish. *Lamina* 12–50 cm long, 3–9 mm wide. *Areolae* in a single row on each side of the midvein. Guatemala to Bolivia, West Indies; from 0 to 1,500 m in Costa Rica, on both slopes.

A canopy or trunk epiphyte, frequent and widespread at La Selva.